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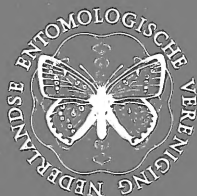
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A journal of systematic and evolutionary
entomology since 1858



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The 'Tijdschrift voor Entomologie' (Netherlands Journal of Entomology) has a long tradition in the publication of original papers on insect taxonomy and systematics. The editors particularly invite papers on the insect fauna of the Palaearctic and Indo-Australian regions, especially those including evolutionary aspects e.g. phylogeny and biogeography, or ethology and ecology as far as meaningful for insect taxonomy. Authors wishing to submit papers on disciplines related to taxonomy, e.g. descriptive aspects of morphology, ethology, ecology and applied entomology, are requested to contact the editorial board before submitting. Usually, such papers will only be published when space allows.

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PTEROPHORUS SCHÄFFER IN THE ETHIOPIAN REGION (LEPIDOPTERA: PTEROPHORIDAE: PTEROPHORINAE): NEW SPECIES AND CHECKLIST

Gielis, C., 1991. *Pterophorus* Schäffer in the Ethiopian region (Lepidoptera: Pterophoridae: Pterophorinae): new species and checklist. – Tijdschrift voor Entomologie 134: 1-8, figs. 1-21. [ISSN 0040-7496]. Published 1 July 1991.

Pterophorus dallastai sp. n., *P. uzungwe* sp. n. and *P. massai* sp. n. are described. A provisional checklist of the Ethiopian *Pterophorus* species is given, with notes on all species. A lectotype is designated for *P. cleronoma* (Meyrick). *P. centrocrates* (Meyrick) is synonymised with *P. rhyparias* (Meyrick). The status of *P. endophaea* (Meyrick) and *P. bacteriopa* (Meyrick) is discussed.

Correspondence: C. Gielis, Mr. Haafkensstraat 36, 4128 CJ Lexmond, The Netherlands.

Keywords. – Lepidoptera; Pterophoridae; *Pterophorus*; new species; Africa.

When the opportunity arose a number of Ethiopian Pterophoridae from the collections of the Zoological Museum of the University of Copenhagen (ZMUC), the Museum National d'Histoire naturelle, Paris (MNHN) and the Royal Museum of Central Africa in Tervuren (MRAC) were examined. The results are here combined with data obtained from the collection of the British Museum of Natural History, London (BMNH), the Instituut voor Taxonomische Zoologie, Amsterdam (ZMAN) and the authors' collection (CG). Some of the specimens resembled, on superficial examination, palaearctic species. A closer examination of these species, however, showed a considerable variability, especially in the genitalia. This was particularly so in the genus *Pterophorus*, the subject of this publication. The species have usually poorly marked wings, which show a colour, ranging from purely white to pale grey-brown. Especially in the group of purely white specimens examination of the genitalia is essential. It is to be expected that more species will be recognized if more material from this region becomes available.

The genus *Pterophorus* has its main distribution centre in the Palaearctic region. A high number of species (approximately 60) is known from West and Central Europe, the Mediterranean area, Turkey and adjacent areas. From there the genus has a continuous distribution into the Southeast Asiatic region. Apart from Africa, further a few species are

recorded from the Pacific area and the new world.

Literature on the african representatives of the genus *Pterophorus* is scattered over a few smaller publications and mainly comprises single descriptions of species, without illustrations of externals or genitalia. Bigot (1969), in his review of the collection of MRAC, describes and illustrates the specimens in this collection, in this way fixing the new species described by him accurately. Since then, Bigot has given his attention mainly to the fauna of Madagascar. Only Arenberger (1986) and Gielis (1990) have published since on the Ethiopian fauna, but on other subfamilies: Agdistinae and Platyptiliinae.

Provisional checklist of Ethiopian *Pterophorus*

Pterophorus Schäffer, 1766

Acipitilia Hübner, [1825]

Merrifieldia Tutt, 1905

Porritia Tutt, 1905

Alucita auct., nec Linnaeus, 1758

1. *albidus* (Zeller, 1852) comb. n.

2. *rhyparias* (Meyrick, 1907) comb. n.

centrocrates (Meyrick, 1933) syn. n.

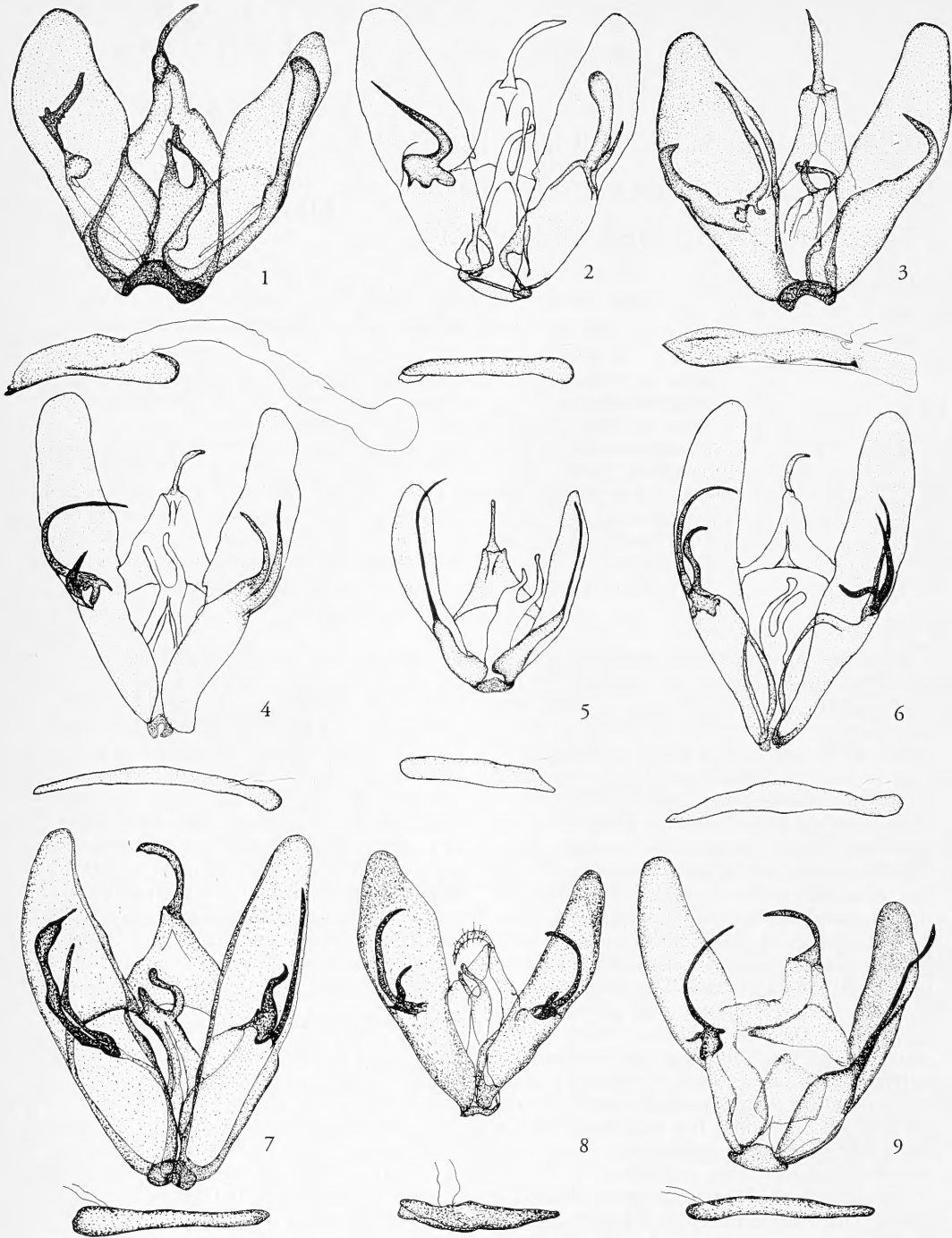
3. *ischnodactyla* (Treitschke, 1833)

4. *endophaea* (Meyrick, 1930) comb. n.

5. *bacteriopa* (Meyrick, 1922) comb. n.

6. *ceraunia* (Bigot, 1969) comb. n.

7. *lampira* (Bigot, 1969) comb. n.



8. *spissa* (Bigot, 1969) comb. n.
9. *lindneri* (Amsel, 1963) comb. n.
10. *candidalis* (Walker, 1864) comb. n.
11. *massai* sp. n.
12. *uzungwe* sp. n.
13. *dallastai* sp. n.
14. *cleronoma* (Meyrick, 1920) comb. n.

TAXONOMIC TREATMENT

Pterophorus Schäffer, 1766

Type-species: *Phalaena Alucita pentadactyla* Linnaeus, 1758

Diagnosis. – Forewing cleft from $\frac{1}{2}$ or less. Top of lobes acute, without a terminal margin. R1 absent, R4 and R5 fused, M3 and CU2 forked or fused. Hindwing without a scale-tooth.

Male genitalia asymmetrical, with asymmetrical costal processes.

Female genitalia with a blister-like bursa copulatrix in which no, one or two signa, an often pronounced vesica seminalis, and often absent apophyses anteriores.

1. *Pterophorus albidus* (Zeller, 1852) comb. n. (figs. 1, 10)

Acipitla albida Zeller, 1852: 397.

Diagnosis. – The species is characterized by the faint yellow colour. Male genitalia with a hooked costal process in the left valve and a large club-like process in the right valve. The female genitalia have the junction between the ductus bursae and the bursa copulatrix in the shape of a bulging protrusion with numerous sclerotized ridges.

Remarks. – This species has originally been described from South Africa. This species can be easily recognized by its yellowish-white to greyish-white colour and the minute punctuation. After studying the male (fig. 1) and female (fig. 10) genitalia, the species turned out to have a wide distribution into the Indo-Australian region. Specimens have been

examined from: Republic of South Africa, Zimbabwe, Kenya, Zaire, Tanzania, Gambia, Côte d'Ivoire, Vietnam, Indonesia, New Guinea.

2. *Pterophorus rhyparias* (Meyrick, 1907) comb. n. (figs. 2, 11)

Alucita rhyparias Meyrick, 1907: 489. Lectotype ♀ (here designated): Rep. of S. Africa, Transvaal, Pretoria (Janse), genitalia slide BM 17993 (BMNH) [examined].

Alucita centrocrates Meyrick, 1933: 425. Holotype ♂: Belgian Congo (Zaire), N.E. Kivu, La Mutura, iii (Seydel), genitalia slide Bigot (MRAC) [examined]. Syn. n.

Diagnosis. – The species is characterized by the pale ochreous-white colour with some small black dots along the costa and dorsum of both forewing lobes. Male genitalia (fig. 2) with a long and short costal process in the left valve and a large club-like process in the right valve. The female genitalia (fig. 11) shows a distinct crescent-shaped distal margin of the 7th tergite and a many folded appearance of the ductus bursae.

Variation. – The colour of the species ranges from grey-white to pale ochreous-white. The number of dots on the forewing may be reduced.

Distribution. – Rep. of S. Africa, Zaire, Kenya, Tanzania.

Remarks. – Since the type-specimens of *P. rhyparias* and *centrocrates* are respectively a female and a male, the synonymy, suggested by Arenberger (personal communication) could only be proven by additional material. The evidence was found in a small series, present in ZMUC, where both sexes are present.

This species is difficult to separate from the next, *P. ischnodactyla* Treitschke, and can only be distinguished by the distinct genitalia.

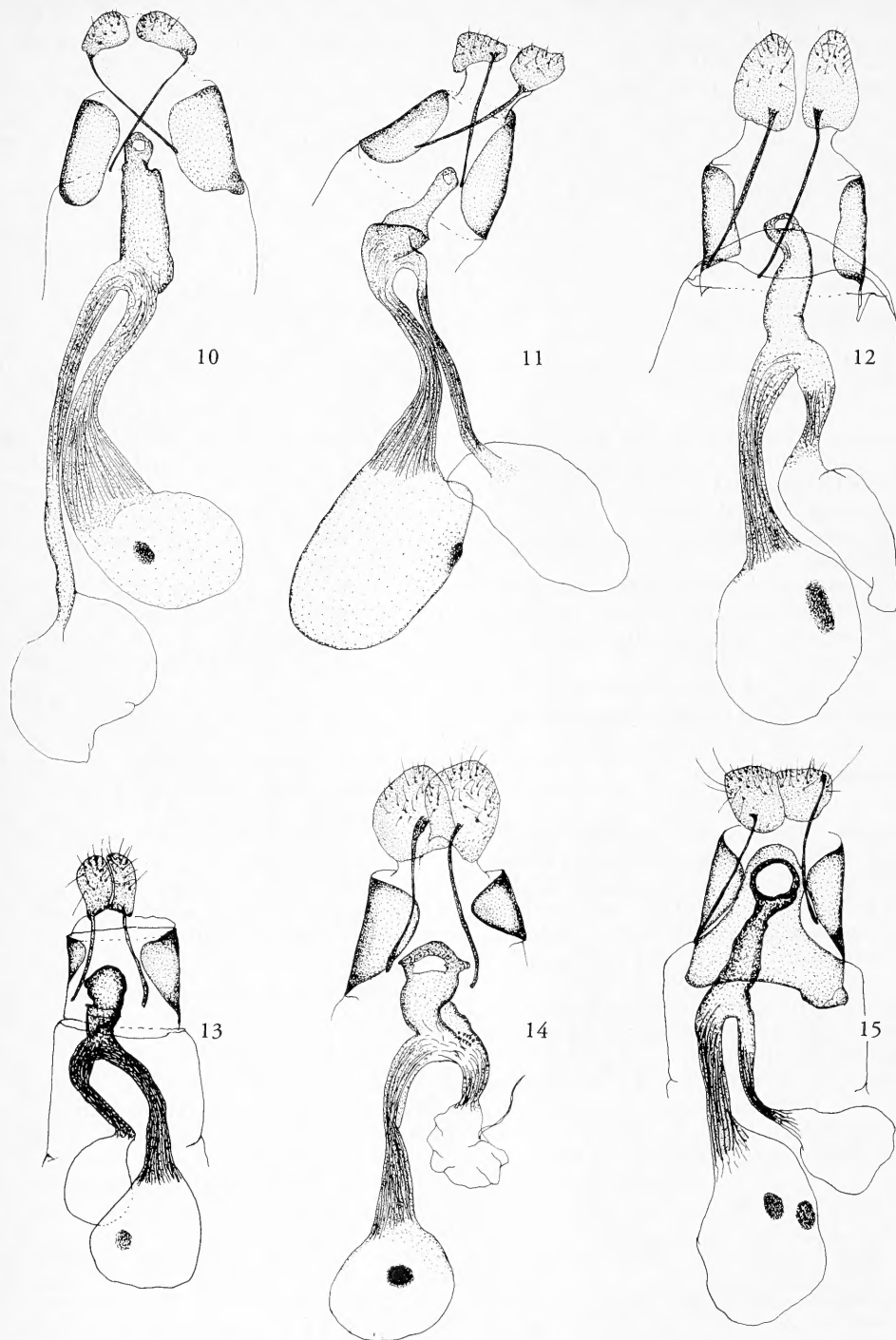
3. *Pterophorus ischnodactyla* (Treitschke, 1833) (fig. 3)

Alucita ischnodactyla Treitschke, 1833: 223.

Diagnosis. – The species is characterized by the pale ochreous-white colour and the small black dots along the costa and dorsum of the forewing. Male genitalia (fig. 3) with a widely forked costal process in the left valve and a hooked single process in the right valve. The female genitalia show an excavated shape of the distal margin of the 7th tergite, the ductus bursae is bulged out, with hardly any transverse ridges.

Remarks. – The Zoological Museum, Amsterdam (ZMAN) holds a specimen from the Republic of South Africa, Bloemfontein, 30.i.1951 (Ee), genitalia CG 1695. This specimen represents the sole verified African record of the species known to me.

Figs. 1-9. *Pterophorus* spp., male genitalia. – 1, *P. albidus* (Zeller) Rep. of S. Africa, slide CG 1694 (ZMAN); 2, *P. rhyparias* (Meyrick), British East Africa, slide CG 1870 (MNHN); 3, *P. ischnodactyla* (Treitschke, 1833). Rep. of S. Africa, slide CG 1695 (ZMAN); 4, *P. ceraunia* (Bigot), paratype, Zaire, slide Bigot (MRAC); 5, *P. lampra* (Bigot), paratype, Zaire, slide Bigot (MRAC); 6, *P. spissa* (Bigot), Central African Republic, slide CG 1878 (MNHN); 7, *P. candidalis* (Walker), Ethiopia, slide CG 1879 (MNHN); 8, *P. dallastai* sp. n., holotype; 9, *P. uzungwe* sp. n., holotype.



Figs. 10-15. *Pterophorus* spp., female genitalia. - 10, *P. albidus* (Zeller), Tanzania, slide CG 4018 (ZMUC); 11, *P. rhymparias* (Meyrick), Zaire, slide Bigot (MRAC); 12, *P. ceraunia* (Bigot), Benin, slide CG 1881 (MNHN); 13, *P. lampra* (Bigot), Côte d'Ivoire, slide CG 2178 (CG); 14, *P. spissa* (Bigot), paratype, Zaire, slide Bigot (MRAC); 15, *P. candidalis* (Walker), Côte d'Ivoire, slide CG 2182 (CG).

This means an extension of the distribution from the Mediterranean area towards the south of Africa.

4. *Pterophorus endophaea* (Meyrick, 1930) comb. n.

Alucita endophaea Meyrick, 1930:576.

Distribution. – Mozambique.

Remarks. – See under *P. bacteriopa*

5. *Pterophorus bacteriopa* (Meyrick, 1922) comb. n.

Alucita bacteriopa Meyrick, 1922: 41.

Distribution. – Tanzania.

Remarks. – *P. endophaea* and *P. bacteriopa* have not been examined, since I was unable to locate the type specimens. The description of both species indicates a relationship with the difficult to separate species *P. rhypharias* and *P. ischnodactyla*. A synonymy based on the descriptions is suggestive, but not proven yet.

6. *Pterophorus ceraunia* (Bigot, 1969) comb. n.
(figs. 4, 12)

Aciptilia ceraunia Bigot, 1969: 204.

Diagnosis. – The species belongs to the group of white species, with distinct black fringe markings. Differs in male genitalia (fig. 4) in having an asymmetrical pair of costal processes in the left valve and an equal long pair of processes in the right valve. In female genitalia (fig. 12) in having long ductal, longitudinally ridged, segments in both the junctions to the bursa copulatrix as to the vesica seminalis. Antrum longitudinal.

Distribution. – Zaire, Benin.

7. *Pterophorus lampra* (Bigot, 1969) comb. n.
(figs. 5, 13)

Aciptilia lampra Bigot, 1969: 204.

Diagnosis. – The forewings are purely white with some black scales near the base and inner margin of the first lobe. Differs in male genitalia (fig. 5) in having a single costal process in the left valve; slightly longer than the valve and a single long costal process in the right valve which is slightly shorter than the valve, in female genitalia (fig. 13) in having an arched 7th tergite, with the lateral positioned antrum, laterally progressing via

the short ductus bursae into the blister-like bursa copulatrix.

Distribution. – Zaire, Gabon, Côte d'Ivoire.

8. *Pterophorus spissa* (Bigot, 1969) comb. n.
(figs. 6, 14)

Aciptilia spissa Bigot, 1969: 202.

Diagnosis. – Forewings pure white, with small black spots at the inner margin of both lobes. The fringes show a distinct black and white pattern. Differs in male genitalia (fig. 6) in having two costal processes in the left valve, of which the shorter is $\frac{2}{3}$ th of the length of the longer. In the right valve two costal processes of equal length and a small transverse, short hook; in female genitalia (fig. 14) in having the ductus bursae slightly longer than the ductus to the vesica seminalis. Antrum large, almost square.

Distribution. – Zaire, Central African Republic.

9. *Pterophorus lindneri* (Amsel, 1963) comb. n.

Aciptilia lindneri Amsel, 1963: 6.

Diagnosis. – The species is shining white, without any dark scales. Bursa copulatrix without a signum.

Male genitalia. – Unknown.

Female genitalia. – See diagnosis.

Distribution. – Ethiopia.

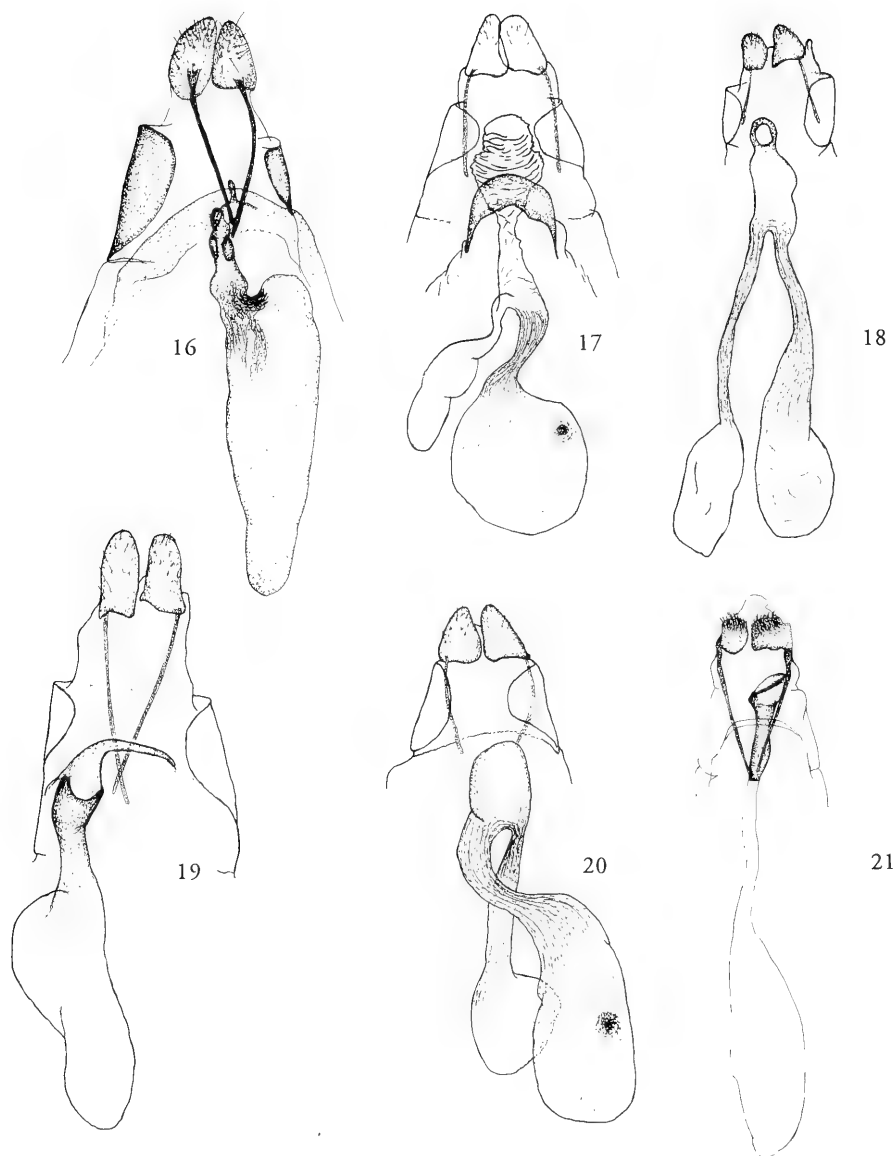
Remarks. – I have not examined the type-specimen, since the description by Amsel (1963) is adequate. It indicates the absence of a signum, which character differentiates the species from all its allies, which have one or two rosette-like signa in their bursa copulatrix.

10. *Pterophorus candidalis* (Walker, 1864) comb. n.
(figs. 7, 15-17)

Acipitilus candidalis Walker, 1864: 948.

Redescription. – Wingspan 15-28 mm. Head white. Palpae short, white and greyish at top. Antennae white, shortly ciliated. Thorax, mesothorax, tegulae and abdomen white. Legs white. Spurs of unequal length. Forewings cleft from $\frac{2}{5}$, colour white with a faint yellowish grey gloss. Sparse dark scales at the base of the cleft and near the apex of the first lobe. Fringes white, at dorsum of both lobes with two faint greyish interruptions. Hindwings white. Fringes white, at dorsum of second lobe a greyish interruption.

Male genitalia (fig. 7). – Valvae asymmetrical. In



Figs. 16-21. *Pterophorus* spp., female genitalia. – 16, *P. candidalis* (Walker), Chad, slide CG 2186 (CG); 17, Idem, Tanzania, slide CG 4020 (ZMUC); 18, *P. dallastai* sp. n., paratype, slide CG 1851 (MRAC); 19, *P. massai* sp. n., holotype, 20; *P. uzungwe* sp. n., paratype, slide CG 4040 (ZMUC); 21, *P. cleronoma* Meyrick, paralectotype, slide Bigot (MNHN).

right valve a pair of saccular spines; the ventral spine twice as long as the centrally placed spine. The left valve with two saccular spines; the ventral spine abruptly ending in a slender, acute top. The dorsal spine slender, length $\frac{4}{5}$ th of the length of the ventral spine. Tegumen simple. Uncus slender, of moderate length. Vinculum arched. Aedeagus straight.

Female genitalia (figs. 15-17). – Antrum in shape of a slender rectangular plate, with a rounded top around a small hole. Ductus bursae and ductus seminalis well-developed with longitudinal ridges. Bursa copulatrix vesicular, with a single rosette-like signum.

Variation. – The female genitalia show variation in the length of the ductus seminalis. In specimens from Côte d'Ivoire (fig. 15) it is longer than the ductus bursae; from Chad and Ethiopia (fig. 16) of equal length, and in Tanzania (fig. 17) shorter than the ductus bursae.

Distribution. – Ethiopia, Kenya, Tanzania, Zaïre, Chad, Côte d'Ivoire, Sierra Leone.

Remarks. – The type specimen from Sierra Leone (BMNH) is missing its abdomen. After comparing with the specimens from areas relatively close to the type locality, I agree with Bigot (1969) about the identity of the species.

11. *Pterophorus dallastai* sp. n. (figs. 8, 18)

Type material. – Holotype ♂: Zaïre [Congo Belge], P. N. A., Secteur Tschiaberimu, Mont Kamatondi près Kizungu, 2850 m., 22.iv.1955 (Vanschuytbroeck & Fontein, no. 12785), genitalia slide CG 1850 (MRAC). – Paratypes: 1 ♀, Zaïre [Congo Belge], P. N. A., Secteur Tschiaberimu, Mont Musimba près Musabaki, 2450 m., 25.iii.1954 (Vanschuytbroeck & Synave, no. 7830), genitalia slide CG 1849 (MRAC); 2 ♀, Zaïre [Congo Belge], P. N. A., Secteur Tschiaberimu, Riv. Musavaki, affl. Talya Nord, 2720 m, 26-29.iii.1954 (Vanschuytbroeck & Synave, no. 7828-29), genitalia slides CG 1851, 1852 (MRAC, CG).

Diagnosis. – The species is closely related to *P. candidalis* (Walker). It is characterized by the slightly ochreous tinge of the forewing, the saccular spines in the male genitalia and the shape of the antrum in the female genitalia.

Description. – Male, female. Wingspan 24-28 mm. External characters as in *P. candidalis* (Walker). The colour of the forewings is slightly ochreous tinged.

Male genitalia (fig. 8). – Valvae asymmetrical. Right valve narrow, lanceolate, with a long curved and a short stout saccular spine. Left valve widening towards $\frac{3}{4}$ th of valve length; with a long curved and a short, wavy saccular spine. Tegumen bilobate. Uncus slender, moderate. Vinculum narrow,

arched. Aedeagus tube-like, towards top gradually narrowing.

Female genitalia (fig. 18). – Antrum large, rounded, without a central hole. Ductus bursae longer than ductus seminalis, both ducti with longitudinal ridges. Bursa copulatrix vesicular, with a single rosette-like signum.

Variation. – The specimens show some variation in the intensity of the black scaling on the forewings.

Biology. – The moths were collected in March and April. Immature stages unknown.

Distribution. – Zaïre.

Etymology. – A noun in genitive case, named in honour of Dr. U. Dall'asta, curator of Lepidoptera in MRAC.

12. *Pterophorus massai* sp. n. (fig. 19)

Type material. – Holotype ♀: Kenya (Afr. Or. Angl.), Nairobi, Plaine Massai, viii.1904 (Alluaud), genitalia slide CG 1875 (MNHN).

Diagnosis. – The species is closely related to *P. candidalis* (Walker) and *P. dallastai* Gielis, but characterized by the female genitalia: the ratio of the length of the ductus bursae and the ductus seminalis is three to one.

Description. – Female. Wingspan 25 mm. External characters as in *P. candidalis* (Walker).

Male genitalia. – Unknown.

Female genitalia (fig. 19). – Antrum large, ending roof-like, with an oval hole. Ductus bursae three times longer than ductus seminalis, both with longitudinal ridges. At the junction of the ductus bursae and ductus seminalis two rows of small spines. Bursa copulatrix vesicular, with a rosette-like signum.

Biology. – The moth was collected in August. Immature stages unknown.

Distribution. – Kenya.

Etymology. – *Massai*, a noun in apposition, named after the type locality.

13. *Pterophorus uzungwe* sp. n. (figs. 9, 20)

Type material. – Holotype ♂: Tanzania, Uzungwe Mts., Mwanihane Forest above Sanje, 1000 m, 1.viii.1981 (Stoltze & Schaff), genitalia slide CG 4039 (ZMUC). Paratype ♀: same locality and data, genitalia slide CG 4040 (CG).

Diagnosis. – The species is characterized by the shape of the saccular arms in the male and the double signum in the female. The size is relatively

small for species of its group.

Description. – Male, female. Wingspan 18-19 mm. External characters as in *P. candidalis* (Walker).

Male genitalia (fig. 9). – Valvae asymmetrical. Right valve with a long, almost straight, saccular spine. Left valve with a curved saccular spine, with two small lateral thorns. Tegumen bilobate. Uncus slender, moderate. Vinculum rather wide. Aedeagus tube-like.

Female genitalia (fig. 20). – Antrum three times longer than wide, club-like, with a large central distal hole. Ductus bursae and ductus seminalis of equal length, both with longitudinal ridges. Bursa copulatrix with two rosette-like signa.

Biology. – The moths were collected in August. Immature stages unknown.

Distribution. – Tanzania.

Etymology. – *Uzungwe*, a noun in apposition, named after the type locality.

14. *Pterophorus cleronoma* (Meyrick, 1920) (fig. 21)

Alucita cleronoma Meyrick, 1920: 41. Lectotype ♀ (here designated): Brit. E. Africa, Kenya, Mt. Kenya, i-ii.1912 (Alluaud & Jeannel), genitalia slide BM 17987 (BMNH) [examined].

Other material examined. – Paralectotype ♀: locality and data as lectotype, genitalia slide Bigot (MNHN) [examined].

Diagnosis. – The species is characterized by the shape of the female genitalia. Especially the gradually narrowing antrum, in combination with the absence of a signum is diagnostic.

Female genitalia (fig. 21). – Antrum gradually narrowing. Ductus bursae slender. Bursa copulatrix vesicular. No signum. Apophyses anteriores absent. Apophyses posteriores three times longer than papillae anales.

Distribution. – Kenya.

Remarks. – In his description Meyrick did not designate a holotype. Both BMNH and MNHN appeared to hold a specimen labelled 'type', the BMNH specimen is herewith designated as lectotype.

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I wish to thank Mr. B. Brugge (ZMAN), Dr. U. Dall'asta (MRAC), Mr. O. Karsholt (ZMUC), Dr. G. C. Luquet (MNHN) and Mr. M. Shaffer (BMNH) for the opportunity to study the Pterophoridae in their museum, Mr. H. W. van der Wolf for correcting the English text and Mrs. van de Sant for typing the manuscript.

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REVIEW OF MALESIAN SPHECINA (HYMENOPTERA, SPHECIDAE, SPHECINAE)

Hensen, R. V., 1991. Review of Malesian Sphecina (Hymenoptera, Sphecidae, Sphecinae). – Tijdschrift voor Entomologie 134: 9-30, figs. 1-65. [ISSN 0040-7496]. Published 1 July 1991.

The species of *Sphex* and *Isodontia* (subtribe Sphecina) in the Malesian region are reviewed. Twenty species are recognized in *Isodontia*, which are segregated into five species-groups, while 21 species are recognized in *Sphex*, divided among three species-groups. Keys are provided to the genera, species-groups and species. Synonymy and distribution of the species is discussed. Twelve new species are described, viz. *I. pilipes* (Burma to Sumatra, Borneo), *I. cestra*, *I. elsei* (both Sulawesi), *I. nidulans* (Philippines), *I. immaculata*, *I. capillata*, *I. delicata*, *I. papua*, *S. wilsoni*, *S. rex* (all New Guinea), *S. solomon* (Solomon Islands), and *S. walsbae* (NE India to Sumatra, Borneo). The following new synonymies are established: *Sphex morosus* Smith, 1861, *S. volatilis* Smith, 1861, *S. triodon* Kohl, 1890, *S. abditus* Kohl, 1895 and *S. abditus nugenti* Turner, 1910 are synonymized with *Isodontia aurifrons* (Smith, 1859); *I. diodon alemon* Van der Vecht, 1957 with *I. severini* (Kohl, 1898); *S. ustulatus* Kohl, 1890, *S. simplex* Kohl, 1898 and *S. insularis* Cameron, 1901 with *I. praslinia* (Guérin-Méneville, 1831); *S. albobirtus* (Turner, 1908) with *I. sepicola* (Smith, 1859) and *S. fulvohirtus* Bingham, 1890 with *S. diabolicus* Smith, 1858.

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Key words. – Malesia, Oriental region, Australian region, Sphecidae, *Sphex*, *Isodontia*, taxonomy.

In this paper the species of the subtribe Sphecina comprising the genera *Sphex* Linnaeus and *Isodontia* Patton are briefly treated as far as they occur in the Malesian area. The Malesian area is used here in a broad sense, i. e. comprising Southern Thailand, Malaysia, Indonesia, the Philippines, New Guinea and the Solomon Islands.

Sphex and *Isodontia* are large, active insects, and some of the species treated here are among the most commonly encountered digger wasps in the area. The last comprehensive publication dealing with the Malesian species was that by Kohl (1890), but the taxonomy of the group was updated in many smaller papers (eg. Kohl 1895, 1898, Van der Vecht 1957, 1973). Therefore, it is surprising that so many new species remained undetected. Furthermore, a considerable number of new synonyms were discovered in the course of this study.

Comprehensive diagnoses of the morphology and biology of the two genera were given by Bohart & Menke (1976), and need not be repeated here. One of the aims of this study is to define and diagnose a number of species-groups. Most of these groups are considered monophyletic, being based on inferred synapomorphies. Others, in particular

the *Sphex subtruncatus*-group are possibly paraphyletic. It seems premature to pay more attention to the phylogeny of the subtribe here, as a thorough treatment of this subject will require study of all species in these genera.

This paper deals strictly with species: it does not present a classification below the species-level. Although past workers (eg. Van der Vecht & Krombein 1955) have recognized subspecies in the Malesian *Isodontia*, especially for colour differences from island to island, I have not recognized them in this paper. Subspecific names recognized in the past are simply treated here as synonyms of the nominate form. On the other hand, several taxa regarded as subspecies in the past are elevated to species rank.

This study was initiated by dr. J. van der Vecht, and in many instances I have relied on his notes concerning literature, type material and specimens. As far as type specimens are concerned, I have indicated examination by Van der Vecht with a single exclamation mark, by myself with a double exclamation mark after the type depository (eg. BMNH!!). A question mark behind an abbreviation of a museum means that a type was looked for but not found in that particular museum.

A few thousand specimens were examined in the course of this study. I have refrained from listing these explicitly, except for the type material of new species. The outlines of distribution, as given for each species are entirely based on examination of specimens by me or by Van der Vecht, except as noted.

Abbreviations. – Names of museums in which types are preserved are abbreviated as follows.

BMNH	Natural History Museum, London, England.
BRI	Biosystematics Research Institute, Ottawa, Canada.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
CAS	California Academy of Sciences, San Francisco, USA.
DEI	Deutsche Entomologische Institut, Eberswalde, Germany.
IRSN	Institut Royal de Sciences Naturelles, Brussels, Belgium.
MCG	Museo Civico di Storia Naturale, Genova, Italy.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
NMB	Naturhistorisches Museum, Basel, Switzerland.
NMW	Naturhistorisches Museum, Vienna, Austria.
OUM	Oxford University Museum, Oxford, England.
RMNH	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.
TMB	Termesztudományi Múzeum, Budapest, Hungary.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA.
UZMC	Universitetets Zoologisk Museum, Copenhagen, Denmark.
ZMB	Zoologisches Museum der Humboldt-universität, Berlin, Germany.

The following morphological terms are abbreviated.

IOC	Shortest interocular distance across the clypeus.
IOV	Shortest interocular distance across the vertex.

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I wish to express my sincere gratitude to these persons, and others who took a constructive interest in my activities. Special thanks are due to Dr. A. S. menke for reviewing the manuscript.

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SYSTEMATIC PART

Key to genera and species-groups

1. Sides of propodeum with complete spiracular groove; basal vein of second submarginal cell as long as or longer than anterior vein; female with well developed tarsal rake, composed of long, flattened spines (fig. 62) (*Sphex*) 2
- Sides of propodeum without spiracular groove; basal vein of second submarginal cell usually shorter than anterior vein; female without tarsal rake (*Isodontia*) 4
2. Metanotum medially with pair of tubercles or with single tubercle, that is more or less impressed medially group of *S. argentatus* (p. 20)
- Metanotum without tubercles, flat or slightly convex medially 3
3. Scutellum of female flat, shiny (sometimes densely covered with tomentum); male flagellum without placoids; claw teeth small, perpendicular to claw (fig. 59) group of *S. resplendens* (p. 22)
- Scutellum of female convex, often with median furrow, usually dull; at least fifth flagellomere of male with placoid (figs. 43-45); claw teeth large, at sharp angle to claw (fig. 60) group of *S. subtruncatus* (p. 26)
4. Males 5
- Females 9
5. Mandibles bidentate 6
- Mandibles tridentate 7
6. Mandibles very slender, nearly straight (fig. 8); inner orbits strongly converging below; petiole

- longer than hind basitarsus; small, slender species, body length 13-19 mm group of *I. diodon* (p. 14)
- Mandibles stout and arcuate (fig. 6); inner orbits parallel or slightly diverging below; petiole shorter than hind basitarsus; large, stout species, body length 20-28 mm group of *I. chrysorrhoea* (p. 13)
7. Fourth flagellomere with well defined placoid (figs. 35-38) group of *I. prasinia* (p. 19)
- Flagellum without placoids 8
8. Basal inner tooth of mandible strongly developed, much stronger than second inner tooth (fig. 10); basal half of clypeus with blunt longitudinal carina group of *I. ochroptera* (p. 19)
- Basal inner tooth of mandibles smaller (fig. 2); basal half of clypeus at most with trace of longitudinal carina group of *I. aurifrons* (p. 11)
9. Widest part of frons slightly narrower than clypeus in the middle, inner orbits slightly diverging below; outer side of hind tibia with more than 20 short spines; body length 29-35 mm group of *I. chrysorrhoea* (p. 13)
- Inner orbits parallel or converging below; outer side of hind tibia with at most 10-12 short spines; body length 14-26 mm 10
10. Mandibles very slender, straight, apically bifid (fig. 7); hind tibiae with 1-3 short spines on outer side; fourth segment of hind tarsi wider than long group of *I. diodon* (p. 14)
- Mandibles robust, curved, apically tridentate (fig. 9); hind tibiae with 5-10 spines on outer side; fourth segment of hind tarsi elongate 11
11. Labrum with single median longitudinal carina, that does not project apically; apical margin of clypeus with pair of well differentiated teeth (fig. 9); pilosity of head and mesosoma black group of *I. ochroptera* (p. 19)
- Labrum apically with two parallel, raised, projecting carinae; apical clypeal margin medially notched (fig. 11), or with pair of short teeth (fig. 1); pilosity variable 12
12. First flagellomere distinctly longer than second; antennae not or hardly longitudinally ridged (fig. 21); mandible stout (fig. 11) group of *I. prasinia* (p. 19)
- First flagellomere hardly longer than second (fig. 19), or (*I. pilipes*) mandibles slender (fig. 3); antennae longitudinally ridged (fig. 19) group of *I. aurifrons* (p. 11)

Genus *Isodontia* Paton

Group of *Isodontia aurifrons*

Diagnosis

Body length ♂ 25-23 mm, ♀ 17-26 mm. Labrum of female with a pair of short parallel projecting carinae apically; mandible tridentate in both sexes, sometimes with weak third inner tooth near apex; clypeus of female with median notch; first flagellomere as long as second; flagellum of female usually with longitudinal sulci on second to tenth segment; third to seventh flagellomere in male with convex, papillate sensory areas; outer side of hind tibia with 5-9 short spines; petiole usually shorter than hind basitarsus.

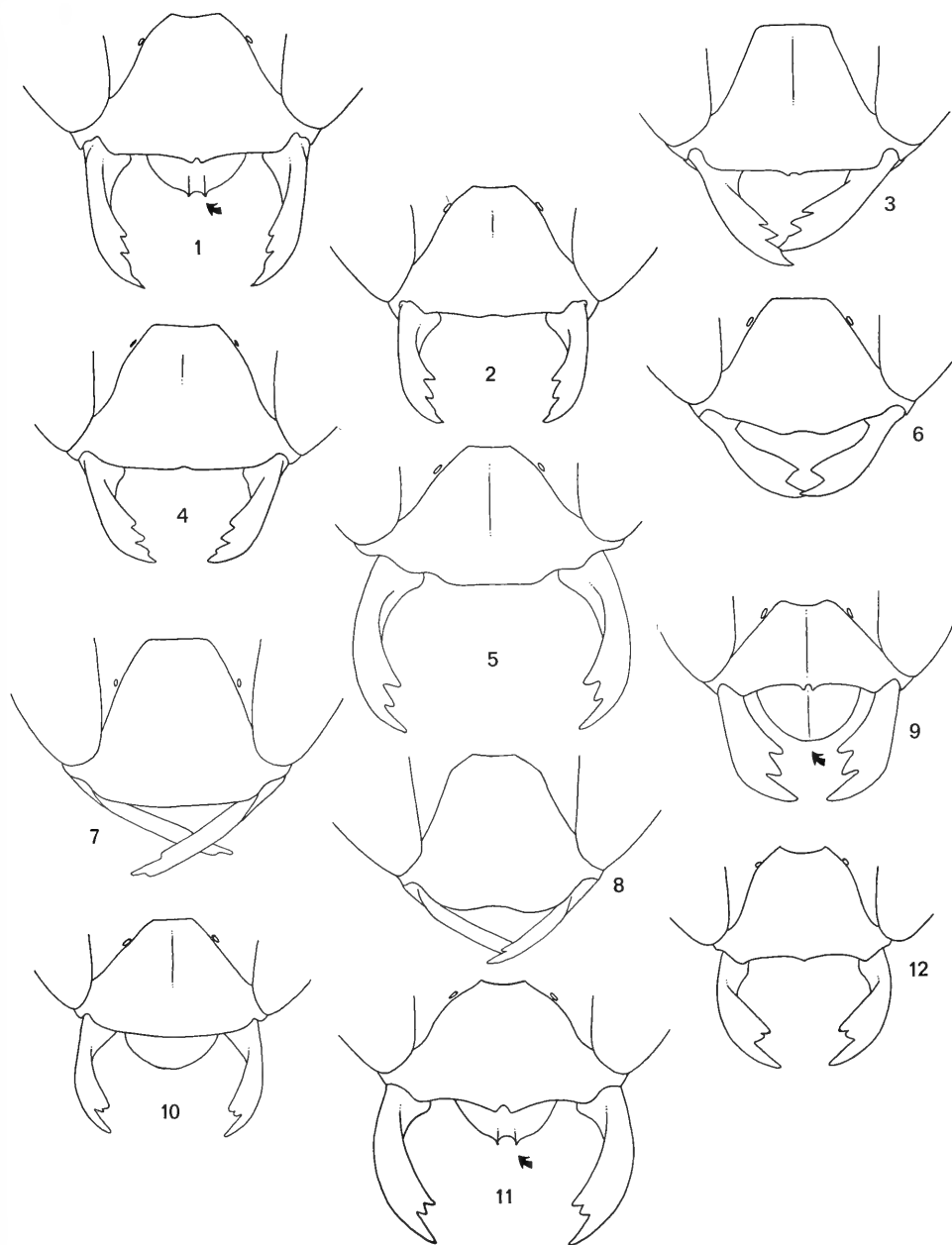
Species included

Species treated. – *I. aurifrons* (Sm.), *formosicola* (Strand), *pilipes* sp. n.

Other included species. – *I. maidli* (Yasumatsu) from Japan.

Key to species

1. Females 2
- Males 4
2. First flagellomere much longer than second (fig. 20); Burma, Sumatra, Borneo *pilipes* sp. n.
- First flagellomere not or scarcely longer than second (fig. 19) 3
3. Metasoma largely or entirely dull red; clypeus with median carina over most of its length; Taiwan, China, S. Thailand, Malaysia, Sumatra, Borneo *formosicola* (Strand)
- Metasoma entirely black; clypeus with short carina near base or medially; Sikkim to China and Malaysia, Malesian region, Queensland *aurifrons* (Smith)
4. Metasoma largely dull red; third flagellomere as long as second (fig. 23); clypeus apically with pair of short teeth; wings yellowish *formosicola* (Strand)
- Metasoma entirely black; third flagellomere longer than second; clypeus apically without teeth (fig. 2); wings brown or clear 5
5. Petiole as long as hind basitarsus; first flagellomere longer than second (fig. 24) *pilipes* sp. n.
- Petiole shorter than hind basitarsus; first flagellomere as long as second (fig. 22) *aurifrons* (Smith)



Figs. 1-12. *Isodontia*, clypeus and mandibles. – 1, *aurifrons*, ♀; 2, *aurifrons*, ♂; 3, *pilipes*, ♀; 4, *pilipes*, ♂; 5, *chrysorrhoea*, ♀; 6, *chrysorrhoea*, ♂; 7, *cestra*, ♀; 8, *delicata*, ♂; 9, *ochroptera*, ♀; 10, *ochroptera*, ♂; 11, *praslinia*, ♀; 12, *praslinia*, ♂.

***Isodontia aurifrons* (Smith)**

(figs. 1-2, 19, 22)

Sphecx aurifrons Smith, 1859: 157. Lectotype ♀ (present designation): Indonesia, Aru (OUM!!)*Sphecx morosus* Smith, 1860: 122. Holotype ♂: Indonesia, Bacan (OUM!!) Syn. n.*Sphecx volatilis* Smith, 1860: 122. Holotype ♀: Indonesia, Bacan (OUM!!) Syn. n.*Sphecx triodon* Kohl, 1890: 377. Lectotype ♂ (present designation): Indonesia, Java (NMW!!) Syn. n.*Sphecx abditus* Kohl, 1895: 51. Holotype ♀: Sikkim (NMW!!) Syn. n.*Sphecx abditus nugenti* Turner, 1910a: 343, 345. Holotype ♀: Australia, Cairns (BMNH!!) Syn. n.

Distribution. – Continental Asia from Southern India and Sri Lanka to China and Malaysia, Indonesia, Philippines, New Guinea, Queensland.

***Isodontia formosicola* (Strand)**

(fig. 23)

Sphecx (Isodontia) formosicola Strand, 1913: 82. Lectotype ♀ (present designation): Taiwan: Hoozan (DEI!!)

Distribution. – Continental Asia from China to Malaysia, Taiwan, Sumatra, Borneo.

***Isodontia pilipes* sp. n.**

(figs. 3-4, 20, 24, 46)

Type material. – Holotype ♂, Indonesia, 'S. Sumatra, + 600 m, Res. Benkoelen, Tandjong Sakti, 16-19 VII, M. E. Walsh leg. 1935' (RMNH). – Paratypes. Burma: Tenasserim, Ihaungyin Valley, v.1893, '*Sphecx aurifrons* Sm., ♂' (1 ♀), Tenasserim, Ataran Valley, xii.1891 (1 ♀), Burma, Middle Tenasserim, Haundraw Valley, viii.1894 (1 ♀), all C. T. Bingham (BMNH). Indonesia: S. Sumatra, Benkulen, 50 m, 19-21.v.1935, M. E. Walsh (1 ♂, RMNH); W. Sumatra, Padangpanjang, 800 m, 1.v.1988, R. Hensen (1 ♂, RMNH). Malaysia: Sabah, Ranau 8 mi. N., Paring Hot Springs, 500 m, 8-11.x.1958, L. W. Quate (1 ♂, BMNH); Borneo, v.1900, P. Cameron coll., '*Sphecx nigripes*, Sm.' (1 ♀, BMNH); Borneo, Kuching, v.1900 (1 ♂, BMNH).

Diagnosis

Within the *aurifrons*-group, *pilipes* is characterized by the first flagellomere being distinctly longer than the second. Additionally, in the male, the petiole is as long as the hind basitarsus (shorter in the other species). *I. pilipes* may actually be closest to the Japanese *I. maidli* (Yasumatsu). It differs from that species in the male by the presence of hair-fringes on the sternites, and in the relative lengths of the proximal flagellomere (1 : 1 : 1.4 in *maidli*). In the female *I. pilipes* is characterized by the dark hind tibiae (reddish in *maidli*) and the presence of transverse rugae medially on the propodeum.

Description

Female. – Body length 17.5-21.0 mm; length of forewing 12.5-15.0 mm. Black, mandible medially reddish, tegulae with margin brownish yellow or reddish, distinctly lighter than the center. Wings yellowish, apical margins and particularly apex of forewing infuscated. Erect pilosity of head and mesosoma brown but yellowish on genae, venter of mesosoma and propodeum. Face with rather sparse silvery tomentum, mesosoma without conspicuous tomentum. Clypeus 0.9 times as long as IOC, with median carina on dorsal half; IOV 1.0 times IOC; relative lengths of flagellomeres I-III 1 : 0.8 : 0.85; mandibles slender. Mesoscutum shiny, sparsely finely punctate, punctures on disc 1-3 diameters apart; propodeal dorsum shiny, rugose-punctate, with short transverse rugae medially. Petiole 0.8 times as long as hind basitarsus.

Male. – Body length 15.0-17.0 mm; length of forewing 11.0-12.5 mm. Like the female, except for the following. Black; mesoscutum with faint greyish shine. Wings light brown, with violaceous shine. Erect pilosity of head brownish to black, of mesosoma yellowish grey, but darker on mesoscutum. Clypeus 0.85 times as long as IOC; IOV 1.0-1.1 times IOC (1.0 in type); relative lengths of flagellomeres I-III 1 : 1.0 : 1.3; flagellomeres III-VIII with convex, papillate sensory areas; mandible with faint third inner tooth near apex; propodeal dorsum finely punctate-reticulate. Petiole 1.0-1.05 times as long as hind basitarsus; fourth to seventh sternite with fringes of appressed brown setosity; gonostyle simple.

Etymology

Pilipes is a noun in apposition, from Latin *pilus* = hair and *pes* = leg.

Group of *Isodontia chrysorrhoea* (Kohl)**Diagnosis**

Body length ♀ 29-34 mm, ♂ 20-28 mm; immediately recognized by their large size, and the presence of yellow bands on the metasoma. Female: labrum not modified; mandible tridentate; clypeus rounded; first flagellomere distinctly longer than second. Male: mandible bidentate; clypeus shallowly emarginate; fourth to sixth flagellomere with broad, convex papillate sensory area.

Species included

Species treated. – *I. chrysorrhoea* (Kohl).

Other included species. – *I. auriptygata* Strand from Taiwan, China and Vietnam.

***Isodontia chrysorrhoea* (Kohl)**

(figs. 5-6, 25)

- Sphex apicalis* Smith, 1856: 253. Holotype ♀: Indonesia, Sumatra (BMNH!!) [non Smith, 1856: 262].
- Sphex (Isodontia) chrysorrhoeus* Kohl, 1890: 371 [new name for *S. apicalis* Smith, 1856: 253].
- Sphex (Isodontia) bewitti* Cameron, 1906: 119. Holotype ♂: Malaysia, Sarawak, Kuching (BMNH!!).

Distribution. – S. Thailand, Indonesia (Sumatra, Java, Borneo, Nias), Malaysia (Sarawak); Philippines (Mindanao).

Group of *Isodontia diodon* (Kohl)

Diagnosis

Body length ♂ 12–18 mm, ♀ 14–19 mm. Labrum of female simple; mandible abnormally slender, nearly straight, bidentate in male, the apex bifid in female and with small outer tooth; clypeus of female simple; relative lengths of flagellomeres variable; flagellum of female without sensory areas; flagellum of male with flat placoids on one or more flagellomeres or with broad, convex, papillate sensory areas. Scutellum and metanotum convex; propodeal dorsum reticulate to transversely strigose; outer side of hind tibia with 1–3 spines. Petiole usually longer than hind basitarsus.

Species included

Species treated. – *I. capillata* sp. n., *cestra* sp. n., *delicata* sp. n., *diodon* (Kohl), *egens* (Kohl), *franzi* (Kohl), *immaculata* sp. n., *papua* sp. n., *permutans* (Turner), *severini* (Kohl).

Other included species. – *I. nigelloides* (Strand) from Sri Lanka and Southern India and an unnamed Australian species.

Key to species

1. Females (unknown: *capillata*, *delicata*, *papua*) 2
- Males (unknown: *franzi*) 8
2. Forewing with sharply differentiated dark mark apically 3
- Forewing darkened apically, but dark area not sharply delimited 6
3. Facial tomentum golden 4
- Facial tomentum silvery 5
4. Petiole as long as hind basitarsus; first metasomal tergite black, laterally reddish translucent; Sulawesi *cestra* sp. n.
- Petiole longer than hind basitarsus; first metasomal tergite red; Sumatra, Java, Borneo, Philippines, Nusa Tenggara, Moluccas *severini* (Kohl)
5. Metasoma, except petiole, entirely red; Borneo *franzi* (Cameron)
- Metasoma black, with at most first tergite and posterior margins of other tergites reddish;

Nepal to China and Singapore *diodon* (Kohl)

6. Facial tomentum golden (except specimens from Gizo Isl.); New Guinea, Solomon Islands *permutans* (Turner)
- Facial tomentum silvery 7
7. Mesosoma with conspicuous silvery tomentum on pronotal lobes, metanotum and sides of propodeum; New Guinea, Bismarck Islands, Biak *egens* (Kohl)
- Mesosoma without silvery tomentum: Bismarck Islands *immaculata* sp. n.
8. Flagellomeres I–II short, III at least twice as long as I (eg. fig. 26) 9
- Flagellomeres I–II longer, III at most 1.5 times as long as I (eg. fig. 27) 14
9. Flagellomeres III–VI with broad, flat placoids over their entire length (figs. 26, 30, 31) 10
- Flagellomere III at most with small apical placoid (figs. 28, 32) 13
10. Posterior tergites with conspicuous, dense yellow pilosity; gonostyles apicodorsally with sharply pointed process (fig. 47); New Guinea *capillata* sp. n.
- Facial tomentum silvery; posterior tergites with sparse white or yellowish pilosity; gonostyles apicodorsally rounded (figs. 52, 54) or with broad angle (fig. 51) 11
11. Mesosoma without tomentum; gonostyles apicodorsally swollen and rounded (fig. 52); Bismarck Islands *immaculata* sp. n.
- Mesosoma with conspicuous silvery or golden tomentum on pronotal lobes, metanotum, sides of propodeum; gonostyles either angularly raised apicodorsally (fig. 51), or simply rounded (fig. 54) 12
12. Gonostyles simply rounded apicodorsally (fig. 54); tomentum of mesosoma golden or (Solomon islands) pilosity brown; New Guinea, Solomon Islands *permutans* (Turner)
- Gonostyles apicodorsally raised into a broad angle (fig. 51); tomentum of mesosoma silvery, pilosity pale; New Guinea, Bismarck Islands, Biak *egens* (Kohl)
13. Flagellomere III with small apical placoid, IV–VI with long, narrow, concave placoids (fig. 28); sternite V–VII with fringes of yellow setosity; New Guinea *delicata* sp. n.
- Flagellomere IV with long, narrow, concave placoid, V with small apical placoid (fig. 32); sternites without fringes, only with sparse yellow pilosity; New Guinea *papua* sp. n.
14. Only flagellomeres IV–V with placoids (fig. 27); Sulawesi *cestra* sp. n.
- Flagellomeres (II–) III–V with broad, convex placoid (figs. 29, 33) 14
15. Flagellomere III 1.4 times as long as I (fig. 33);

lower apical angle of gonostyle acute (fig. 50); facial tomentum usually silvery; Nepal to China and Singapore *diodon* (Kohl)

- Flagellomere III 1.1-1.2 times as long as I (fig. 29); lower apical angle of gonostyle a right angle (fig. 55); facial tomentum golden or pale golden; Sumatra, Borneo, Java, Nusa Tenggara, Moluccas, Philippines *severini* (Kohl)

Isodontia capillata sp. n.

(figs. 26, 47)

Type material. - Holotype ♂, Indonesia, Irian Jaya, Jayapura, xii.1936, W. Stüber (RMNH). - Paratypes: Indonesia: Irian Jaya, Jayapura, vii.1938, L. J. Toxopeus (1 ♂, RMNH). Papua New Guinea: Madang Province, Duru, 15 km SW. Madang, ca. 5°20' S, 145°43' E, 14.iii.1987, W. J. Pulawski (1 ♂, CAS).

Diagnosis

Differing from all other species of this group by the dense yellow pilosity covering the posterior tergites, and by the shape of the gonostyles (fig. 47).

Description

Male. - Body length 15.0-16.5 mm, length of forewing 11.0-12.0 mm. Black; mesoscutum with fine oily shine; posterior margins of tergites broadly reddish to yellowish translucent. Wings light brownish hyaline, apically infuscated. Erect pilosity of head and mesosoma yellow; facial tomentum golden; mesosoma with conspicuous golden tomentum on pronotum, sides of mesoscutum, metanotum, mesopleuron and sides of propodeum; metasoma with very conspicuous pale yellow pilosity, dense and erect on posterior tergites. Clypeus 1.0 times as long as IOC, with vague median carina; IOV 1.1 times IOC; relative lengths of flagellomeres I-III 1: 1.4: 2.6; third to sixth flagellomere with broad flat placoid. Mesoscutum densely rather finely punctate, punctures on disc 0.5-1 diameter apart; propodeal dorsum shiny, anteriorly transversely strigose, posteriorly very densely punctate. Petiole 1.2 times as long as hind basitarsus; sternites without fringes, only seventh sternite with some longer pilosity; eighth sternite apically truncate; gonostyle apically with strong tooth pointing upward.

Etymology

Capillata is an adjective, from Latin *capillatus* = long-haired.

Isodontia cestra sp. n.

(figs. 7, 27, 48)

Type material. - Holotype ♀, 'Indonesia, N. Sulawesi, 100 m, Tangkoko-Dua Saudara N. R., 1°30' N, 125°10' E, 28.XI.1985, C. v. Achterberg, RMNH'86' (RMNH). - Paratypes: Indonesia, Sulawesi: Dumoga-Bone N. P., ca. 220 m, nr. Base Camp Toraut R., 0°34' N, 123°54' E, 10.xi.1985, C. v. Achterberg (1 ♀, RMNH); Kendari, iv.1874, O. Beccari (1 ♀, MCG); North Sulawesi, Toli-Toli, xi-xii.1895, H. Fruhstorfer (2 ♂, IRSN, RMNH); 47 km WSW Kotamobagu, Dumoga Bone N. P., Toraut, 211 m, vi.1985, G. R. Else (2 ♀ 4 ♂, BMNH, RMNH); Mt. Sapotan, viii.1937, C. T. & B. B. Brues (1 ♀, MCZ).

Diagnosis

Similar to *severini* and *diodon*; the female differs in having the petiole as long as hind basitarsus (longer in *diodon* and *severini*), the male has the placoids restricted to 4th and 5th flagellomere, and the gonostyles differ markedly in shape.

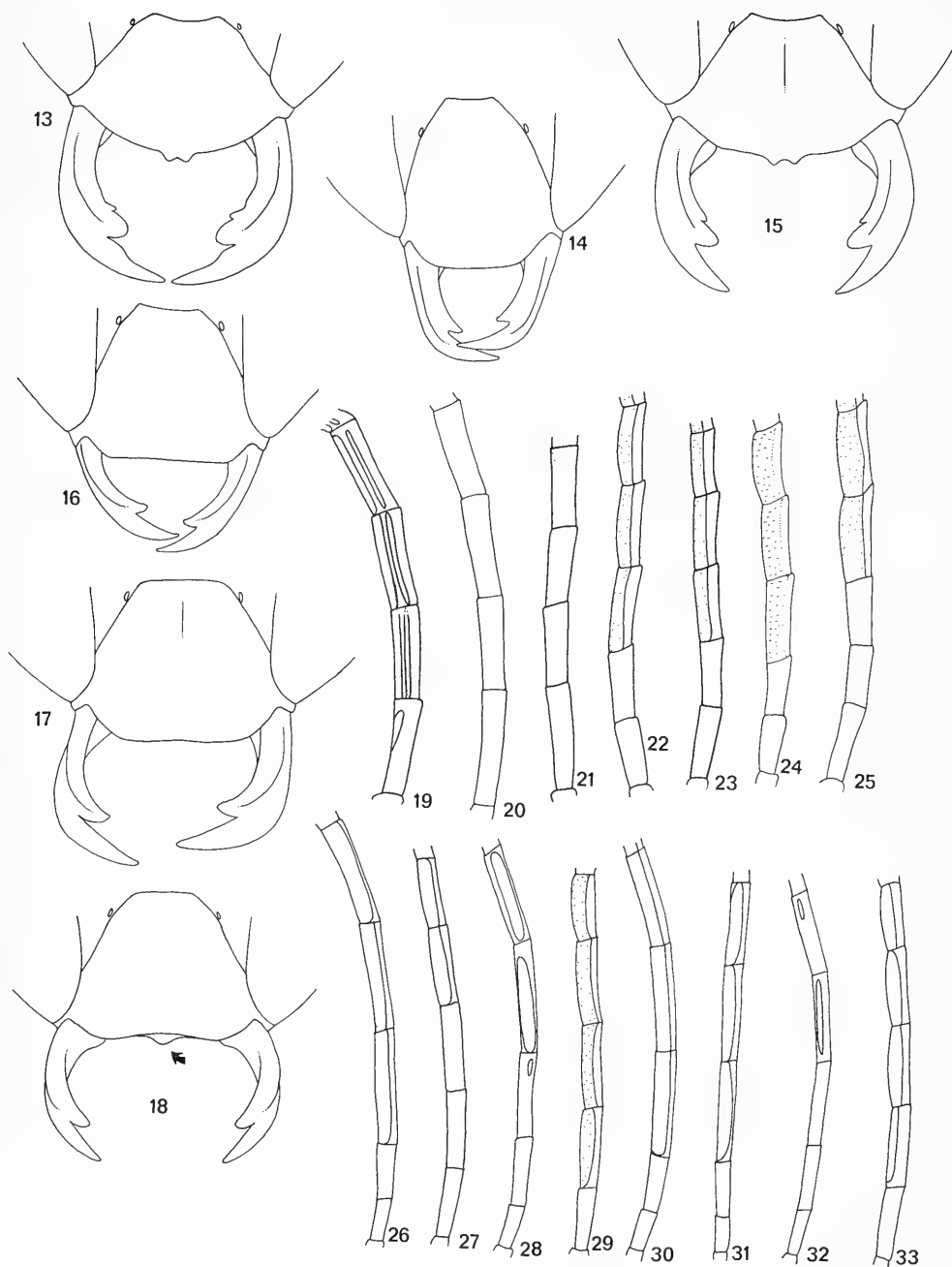
Description

Female. - Body length 15.5-18.5 mm, length of forewing 11.5-13.0 mm. Black; mesoscutum with oily shine; posterior margins of tergites brown. Wings yellowish, with sharply defined dark mark apically. Erect pilosity of head and mesosoma yellow; facial tomentum golden; mesosoma with conspicuous golden tomentum on pronotum, sides of mesoscutum, mesopleuron, metanotum, and sides and declivity of propodeum. Clypeus 1.1 times as long as IOC, without median carina; IOV 1.1 times IOC; relative lengths of flagellomeres I-III 1: 0.8: 0.9. Mesoscutum densely rather coarsely punctate, punctures on disc 0.5-1 diameter apart; propodeal dorsum shiny, rather coarsely rugose-punctate. Petiole 0.95-1.05 times as long as hind basitarsus.

Male. - Body length 14.5-17.0 mm, length of forewing 10.5-12.0 mm. Like the female, except for the following. Erect pilosity of head and mesosoma white; facial tomentum silvery; mesosoma without conspicuous tomentum. Clypeus with vague median carina; IOV 1.2 times IOC; relative lengths of flagellomeres I-III 1: 1.0: 1.15; fourth and fifth flagellomere with broad convex sensory area. Mesoscutum sparsely rather coarsely punctate, punctures on disc 1-2 diameters apart. Petiole 1.05 times as long as hind basitarsus; eighth sternite apically angularly emarginate; gonostyle in lateral view strongly constricted in the middle, apically swollen.

Etymology

Cestra is an arbitrary combination of letters, to be treated as a noun in apposition.



Figs. 13-33. 13-18, *Sphex*, clypeus and mandibles. – 13, *muticus*, ♀; 14, *muticus*, ♂; 15, *solomon*, ♀; 16, *solomon*, ♂; 17, *praedator*, ♂; 18, *walshae*, ♂. 19-33, *Isodontia*, proximal flagellomeres. – 19, *aurifrons*, ♀; 20, *pilipes*, ♀; 21, *prasilinia*, ♀; 22, *aurifrons*, ♂; 23, *formosicola*, ♂; 24, *pilipes*, ♂; 25, *chrysorrhoea*, ♂; 26, *capillata*, ♂; 27, *cestra*, ♂; 28, *delicata*, ♂; 29, *diodon*, ♂; 30, *egens*, ♂; 31, *immaculata*, ♂; 32, *papua*, ♂; 33, *severini*, ♂.

Isodontia delicata sp. n.

(figs. 8, 28, 49)

Type material. – Holotype ♂, Indonesia, Irian Jaya, Jayapura, vii.1938, L. J. Toxopeus, Neth. Ind.-Amer. New Guinea Exp. 1939-39 (RMNH). – Paratypes: Indonesia: same data as holotype (5 ♂, RMNH, BMNH); same locality, vi.1937 (1 ♂), xii.1936 (2 ♂), W. Stüber (RMNH).

Diagnosis

Similar to *papua* (male, female in both species unknown), with which it shares the combination of extremely short flagellomeres I-III, and long narrow concave placoid on fourth flagellomere; *delicata* however has similar placoids on fifth and third flagellomere, and fringes of yellow setosity on the posterior tergites; these traits are lacking in *papua*.

Description

Male. – Body length 13.5-15.5 mm, length of forewing 10.5-11.5 mm. Black; mesoscutum with oily shine; sides of first tergite and posterior margins of other tergites and sternites reddish. Wings slightly yellowish hyaline, apically infuscated. Erect pilosity of head and mesosoma yellow; facial tomentum golden; mesosoma with conspicuous golden tomentum on pronotum, sides of mesoscutum, mesopleuron, sides of propodeum; fourth to eighth sternite with fringes of yellow setosity. Clypeus 1.0 times as long as IOC, with vague median carina; IOV 1.0 times IOC; relative lengths of flagellomeres I-III 1: 1.5 : 2.1; third flagellomere with small apical placoid, fourth to sixth with narrow concave placoid. Mesoscutum densely rather coarsely punctate, punctures on disc 0.5-1 diameter apart; propodeal dorsum shiny, anteriorly transversely strigose, posteriorly punctate-strigose. Petiole 1.2-1.3 times as long as hind basitarsus; eighth sternite truncate; gonostyle simple.

Etymology

Delicata is an adjective, from Latin *delicatus* = delicate.

Isodontia diodon (Kohl)

(figs. 29, 50)

Spheg (*Isodontia*) *diodon* Kohl, 1890: 377. Lectotype ♂ (present designation): 'Celebes, Sumatra' (NMW!!)
Spheg maia Bingham, 1894: 379. Syntypes, ♂, ♀: Burma, Tenasserim (BMNH!!).

Distribution. – This species occurs on the Asian continent, from Nepal to China and Peninsular Malaysia.

Notes. – 1. The lectotype of *Spheg diodon* Kohl is a male, labelled 'Stevens, 860', '*diodon* typ, det Kohl' (NMW). Kohl gave as the habitat of the spe-

cies 'Celebes, Sumatra', but this is almost certainly incorrect. The species that corresponds to both the type and the description is found only on the Asian continent.

2. *I. diodon* has been regarded as a polytypic species by past workers (Van der Vecht 1957, Bohart & Menke 1976). However, typical *I. diodon* differs in several morphological aspects from the forms associated with it in the past. *I. nigelloides* (Strand) is a distinct species. Three other forms are treated here as belonging to *I. severini* (Kohl). The three species are allopatric: *I. nigelloides* [stat. n.] is restricted to Southern India and Sri Lanka; *I. diodon* occurs on the Asiatic mainland from Nepal to China and Malaysia, whereas *I. severini* occurs in the Archipelago.

Isodontia egens (Kohl)

(figs. 30, 51)

Spheg (*Isodontia*) *egens* Kohl, 1898: 335. Holotype ♂: New Britain, Kinigunang (TMB!!).

Distribution. – New Britain, Western New Guinea, Biak.

Isodontia franzi (Cameron)

Spheg (*Isodontia*) *franzi* Cameron, 1902: 246. Holotype ♂: Borneo (BMNH!!).

Distribution. – Only the type specimen from Borneo is known.

Isodontia immaculata sp. n.

(figs. 31, 52)

Type material. – Holotype ♂, Papua New Guinea, New Ireland, Trail to Lelet, Plateau near Danum, 15.xii.1969, J. E. Tobler (CAS). – Paratypes: Papua New Guinea: same data as holotype (2 ♂, CAS, RMNH); Lavongai [New Hanover], Banatam, 24.iii.1962, Noona Dan Exp. (1 ♀, UZMC).

Diagnosis

Within the *diodon*-group, this species is the least tomentose one: the facial tomentum is very sparse and silvery, the mesosoma lacks tomentum, whereas all other species have conspicuous spots of silvery or golden tomentum on pronotal lobes, angles of propodeum, etc. Structurally, the species is similar to *egens* and *permutans*, males of these species share the combination of extremely short proximal flagellomeres, and broad flat placoids on third to sixth flagellomere; *immaculata* differs markedly in the shape of the male gonostyle.

Description

Female. – Body length 17.5 mm, length of forewing 12.5 mm. Black. Wings clear, forewing anteriorly and apically infuscate, the dark mark not sharply delimited. Erect pilosity of head and mesosoma white; facial tomentum silvery, sparse; mesosoma without tomentum. Clypeus 1.1 times as long as IOC, without median carina; IOV 1.0 times IOC; relative lengths of flagellomeres I-III 1: 0.95 : 1.0. Mesoscutum densely rather coarsely punctate, punctures on disc 0.5-1 diameter apart; propodeal dorsum shiny, rather coarsely rugose-punctate. Petiole 1.1 times as long as hind basitarsus.

Male. – Body length 16.0 mm, length of forewing 11.5 mm.

Like the female except for the following. Clypeus 1.1 times as long as IOC, with vague median carina; relative lengths of flagellomeres I-III 1: 1.4 : 2.4; third to sixth flagellomere with broad flat sensory area. Mesoscutum densely rather coarsely punctate, punctures on disc 1-1.5 diameters apart; propodeal dorsum shiny, rather coarsely rugose-punctate. Petiole 1.1 times as long as hind basitarsus; eighth sternite apically not emarginate; gonostyle apico-dorsally swollen and rounded.

Etymology

Immaculata is an adjective, from Latin *immaculatus* = immaculate.

Isodontia papua sp. n.

(figs. 32, 53)

Type material. – Holotype ♂, Indonesia, New Guinea, 'Neth. Ind.-American New Guinea Exped., Araucaria Camp, 800 m, 30.III.1939, L. J. Toxopeus' (RMNH).

Diagnosis

Similar to *delicata* (male, female of both species unknown), with which it shares the combination of extremely short proximal flagellomeres, and a long narrow, concave placoid on the fourth flagellomere. However, *delicata* has similar placoids on fifth and sixth flagellomere, whereas *papua* only has a vestigial one on fifth, and none on sixth. Additionally, *papua* lacks fringes of yellow setosity on the sternites, as found in *delicata*.

Description

Male. – Body length 15.0 mm, length of forewing 11.5 mm. Black; mesoscutum with oily shine; posterior margins of tergites and sternites reddish to yellow. Wings light brownish hyaline, apically infuscated. Erect pilosity of head and mesosoma yellow; facial tomentum silvery; mesosoma with conspicuous golden tomentum on pronotum, sides of mesoscutum, mesopleuron, etc.; posterior tergites

with appressed pale yellow pilosity. Clypeus 1.0 times as long as IOC, with vague median carina; IOV 1.1 times IOC; relative lengths of flagellomeres I-III 1: 1.45 : 2.0; fourth flagellomere with long, narrow, concave placoid, fifth with small apical placoid. Mesoscutum densely rather coarsely punctate, punctures on disc 0.5-1 diameter apart; propodeal dorsum shiny, anteriorly transversely punctate-strigose, posteriorly reticulate-punctate. Petiole 1.2 times as long as hind basitarsus; sixth to eighth sternite with scattered pilosity posteriorly, without real fringes; eighth sternite truncate; gonostyle simple.

Etymology

Papua is noun in apposition, it is the common name for the native inhabitants of New Guinea.

Isodontia permutans (Turner)

(fig. 54)

Sphex permutans Turner, 1912: 198. Lectotype ♀ (present designation): New Guinea, Wataikwa River (BMNH!!)

Distribution. – New Guinea, Solomon Islands.

Notes. – 1. The males of *permutans* and its closest relatives are all easily recognized using characters of the genitalia and secondary sexual characters. The females of *permutans*, *papua*, *delicata*, and *capillata* are apparently inseparable. As the type of *permutans* is a female, the identity of this species is uncertain. I have associated the most common and widely distributed type of male with *permutans*, and described the others as new species. I have not been able to associate females with these. If characters are eventually found to identify females of these species, my interpretations may need revision.

2. *I. permutans* is geographically variable with respect to the colour of pilosity and tomentum. Typically (New Guinea) the pilosity is pale yellow, the tomentum golden. Specimens from Bougainville are similar to the typical form. The pilosity of head and mesosomal dorsum is partly to entirely dark in specimens from the other Solomon Islands. The tomentum is silvery in specimens from Gizo, Kolombangara, San Cristobal, and Malaita.

Isodontia severini (Kohl) stat. rev.

(figs. 33, 55)

Sphex (*Isodontia*) *severini* Kohl, 1898: 337, ♀. – Java (IRSN).

Sphex malayanus Cameron, 1902: 134. Lectotype ♂ (present designation): Borneo, Kuching (BMNH!!)

Sphex (*Isodontia*) *severini* var. *philippensis* Rohwer, 1921: 669. Holotype ♀: Palawan (USNM!!).

Isodontia diodon alemon Vecht, 1957: 367. ♂: Sumba (NMB) Syn. n.

Distribution. – Malaysia, Singapore, Indonesia (Sumatra, Java, Borneo, Sumba, Halmahera), Philippines.

Group of *Isodontia ochroptera*

Diagnosis

Body length ♂ 16-22 mm, ♀ 20-22 mm. Labrum of female with median carina; mandible in both sexes tridentate, basal inner tooth in male strongly developed, projecting beyond second inner tooth; clypeus of female with pair of apical teeth medially; first flagellomere in female distinctly longer than second, in male first and second flagellomere equally long; third to eighth flagellomere of male with broad, convex, papillate sensory areas; antenna of female without sensory areas; outer side of hind tibia with five spines; petiole a little shorter than hind basitarsus.

Species included

Species treated. – *I. ochroptera* (Kohl).

Other included species. – *I. sonani* (Tsuneki) from Taiwan.

Isodontia ochroptera (Kohl)

(figs. 9-10, 34)

Spheg (*Isodontia*) *ochropterus* Kohl, 1890: 378. ♀: Indonesia, Sulawesi, Bantimurung (Mus. Dresden, probably destroyed).

Distribution. – Continental Asia from Eastern India to Laos and Malaysia, Indonesia (Sumatra, Borneo, Java, Sulawesi, Aru, Halmahera), Philippines (Palawan, Samar)

Group of *Isodontia prasinia*

Diagnosis

Body length ♂ 15-23 mm, ♀ 16-23 mm. Labrum of female with a pair of short, parallel, projecting carinae apically; mandible of both sexes tridentate, basal inner tooth strongly developed, projecting beyond second inner tooth; clypeus of female with median notch; first flagellomere longer than second; flagellum of male with generally with flat placoids on flagellomeres IV-VI; antenna of female without sensory areas. Scutellum and metanotum convex; propodeal dorsum more or less reticulate; outer side of hind tibia with 5-10 spines. Petiole usually shorter than hind basitarsus.

Species included

Species treated. – *I. elsei* sp. n., *jaculator* (Smith), *nidulans* sp. n., *praslinia* (Guérin-Méneville), *sepicola* (Smith).

Other included species. – *I. obscurella* (Smith) from Australia, *I. xanthognatha* (Pérez) (= *nigella* (Smith), nec Lichtenstein) [stat. n.] from continental Asia.

Key to species

1. Pilosity of head and mesosoma dark brown to black; wings dark brown with violaceous shine; Timor (?), New Guinea and neighbouring islands *praslinia* (Guérin-Méneville)
– Erect pilosity of head and mesosoma white to yellowish; colour of wings variable 2
2. Propodeal dorsum sparsely punctate, interspaces smooth, shiny; interocular distance across vertex shorter than across clypeus; Philippines *nidulans* sp. n.
– Propodeal dorsum punctate-reticulate to strigose-punctate, more or less dull, without smooth interspaces 3
3. Facial tomentum sparse, silvery, sculpture of clypeus easily visible; Moluccas *jaculator* (Smith)
– Facial tomentum dense, golden or silvery, sculpture of clypeus largely obscured 4
4. Petiole of female 0.8-0.95, of male 0.9-1.0 times as long as hind basitarsus; IOV 0.85-1.05 times IOC; male: mandibles entirely bright reddish; New Guinea and neighbouring islands, Northern Australia *sepicola* (Smith)
– Petiole of female 0.95, of male 1.05-1.1 times as long as hind basitarsus; IOV 1.1 times IOC; male: basal third of mandibles black; Sulawesi *elsei* sp. n.

Isodontia elsei sp. n.

(fig. 35)

Type material. – Holotype ♂, Indonesia, Sulawesi, 'Rosenberg, Toelabella, Celebes' (RMNH). – Paratypes. Indonesia, Sulawesi: Gorontalo (1 ♂), Kwadang (1 ♂), both Rosenberg (RMNH); Patunuang, i.1896, H. Frühstorfer (2 ♀, RMNH); 47 km WSW Kotamobagu, Dumoga Bone N. Pk., Toraut (Forest Edge), 211 m, v-vi.1985, G. R. Else (6 ♂, 3 ♀, BMNH, RMNH); Luwuk, Matanyo Forest, N. of Kayutano, 120 m, 20.x.1989, C. van Achterberg & M. Tulung (1 ♀, RMNH).

Diagnosis

Very similar to *sepicola*, from which it differs only in the characters mentioned in the key.

Description

Female. – Body length 19.0-20.5 mm; length of forewing 13.5-15.5 mm. Black; mesoscutum with

oily shine. Wings light brownish, apical margins more strongly infuscated, with violaceous shine. Erect pilosity of head and mesosoma nearly white; facial tomentum golden, dense, leaving sculpture of clypeus visible under a certain angle only; mesosoma without conspicuous tomentum. Clypeus 0.8 times as long as IOC, without discernable median carina; IOV 1.1 times IOC; relative length of flagellomeres I-III 1 : 0.8 : 0.8. Mesoscutum shiny, sparsely finely punctate, punctures on disc 1-3 diameters apart; propodeal dorsum more shiny than in *I. sepicola*, weakly transversely rugose and shallowly punctate. Petiole 0.95 times as long as hind basitarsus.

Male. – Body length 15.5-20.5 mm; length of forewing 13.5-15.5 mm. Like the female except for the following. Black; mandibles with short reddish zone just before apex. Wings brownish hyaline, apical margins infuscated. Erect pilosity of head and mesosoma yellowish to white. Clypeus 0.85 times as long as IOC; relative length of flagellomeres I-III 1 : 0.8 : 0.85. Petiole 1.05-1.1 times as long as hind basitarsus; third to seventh sternite with fringes of brown setosity; gonostyle simple.

Etymology

Elsei is a noun in the genitive case, referring to Mr. George R. Else, collector of most of the type series, and many other interesting Sulawesi wasps.

***Isodontia jaculator* (Smith)**

(fig. 36)

Sphex jaculator Smith, 1860: 122. Holotype ♂: Indonesia, Bacan (OUM!!).

Distribution. – Exclusively known from the island Bacan, in the Indonesian Northern Moluccas.

***Isodontia nidulans* sp. n.**

Type material. – Holotype ♀, Philippines, Luzon, 'Olongapo, P. I., Subic Bay, V.1967', 'Coll. by J. C. Thomson' (USNM).

Diagnosis

Immediately separated from other species of this group by its very fine sculpture; in particular the propodeal dorsum is smooth, shiny, with sparse fine punctuation.

Description

Female. – Body length 20.0 mm; length of forewing 15.5 mm. Black; mesoscutum with oily shine. Wings brown, with violaceous shine. Erect pilosity of head and mesosoma white; facial tomentum silvery, sparse; mesosoma without conspicuous to-

mentum. Clypeus 0.7 times as long as IOC, with blunt median carina on dorsal half; IOV 0.95 times IOC; relative length of flagellomeres I-III 1 : 0.75 : 0.75. Mesoscutum shiny, obsoletely punctate; propodeal dorsum shiny, along anterior margin with weak rugae, remaining part smooth, finely, shallowly punctate. Petiole 0.9 times as long as hind basitarsus.

Etymology

Nidulans is an adjective based on the Latin verb *nidulare* = to shine.

***Isodontia prasinia* (Guérin-Ménéville)**

(figs. 11-12, 21, 37)

Sphex prasinus Guérin-Ménéville, 1831: pl. 8. Holotype ♀: New Ireland, Pt. Praslin (MCG!).

Sphex (Isodontia) ustulata Kohl, 1890: 378. Holotype ♀: Timor (NMW!!). Syn. n.

Sphex (Isodontia) simplex Kohl, 1898: 334. Lectotype ♂ (present designation): New Guinea: Erima, Astrolabe-Bay (TMB!!). Syn. n.

Sphex (Isodontia) insularis Cameron, 1901: 240. Holotype ♂: New Britain (BMNH!!). Syn. n.

Distribution. – This species occurs on New Guinea and neighbouring islands: New Britain, New Ireland, Misool Island, the Solomon Islands. The record from Timor is based only on the type of *ustulata*, and it is doubtful whether the species indeed occurs there. Species whose occurrence is centered on the Papuan subregion, like *I. prasinia*, and also for example *I. sepicola* and *S. cognatus* rarely occur in the Lesser Sunda islands. The two areas are climatically quite different.

***Isodontia sepicola* (Smith)**

(fig. 38)

Sphex sepicola Smith, 1859: 158. Lectotype ♀ (present designation): Aru (OUM!!)

Sphex albobirtus Turner, 1908: 466. Lectotype ♀ (present designation): Australia: Mackay (BMNH!!). Syn. n.

Distribution. – This species occurs on New Guinea, and neighbouring islands: Aru islands, Solomon islands, Misool, and in Australia, where it seems to be restricted to Northern Queensland.

Genus *Sphex* Linnaeus

Group of *Sphex argentatus*

Diagnosis

Body length ♂ 20-28 mm, ♀ 23-34 mm. Mandible of both female and male bidentate; antenna of

male with placoid(s), at least on fifth flagellomere; scutellum convex, medially impressed; metanotum medially raised into a pair of tubercles, or into a single medially impressed tubercle; claw teeth large, at sharp angle to claw.

Species included

Species treated. – *S. alacer* Kohl, *argentatus* Fabricius, *diabolicus* Smith, *finschii* Kohl, *madasummae* Van der Vecht, *sericeus* Fabricius

Other included species. – *carbonicolor* Vecht, *decoratus* Smith, *ephippium* Smith, *modestus* Smith (all Australian), *fumicatus* Christ (Africa to SW. India and Sri Lanka).

Key to species

1. Propodeal dorsum with 4-6 transverse ridges 2
- Propodeal dorsum without ridges 3
2. Female: apical margin of clypeus with median tooth; male: 2nd to 6th flagellomere with broad placoid (fig. 39); New Guinea *alacer* Kohl
- Female: apical margin of clypeus without tooth; male: 3rd or 4th to 6th flagellomere with placoid (fig. 42); Sri Lanka to New Guinea *sericeus* (Fabricius)
3. Wings uniformly dark brown, with violaceous effulgence; Burma to New Guinea, Philippines *madasummae* Van der Vecht
- Wings clear or yellowish, only at basis and apex sometimes darkened 4
4. Wings strongly yellowish to yellow-brown; Sri Lanka to Sulawesi *diabolicus* Smith
- Wings essentially clear, infusate at base and apex 5
5. Metanotum with single medially impressed tubercle; male: 4th to 6th flagellomere with broad placoids (fig. 41); Moluccas, New Guinea, Solomon Islands, Australia *finschii* Kohl
- Metanotum strongly bituberculate; male: only 5th flagellomere with narrow placoid (fig. 40); widespread *argentatus* Fabricius

Sphex alacer Kohl

(fig. 39)

Sphex alacer Kohl, 1895: 54. Holotype ♀: New Guinea (NMW!).

Distribution. – New Guinea, New Ireland.

Sphex argentatus Fabricius

(fig. 40)

Sphex argentatus Fabricius, 1787: 274. Lectotype ♀ (designated by Van der Vecht 1961: 28): India, Coromandel (Mus. Lund!).

Sphex umbrosus Christ, 1791: 293, pl. 29. No locality given [type lost].

Sphex argenteus Turton, 1800: 485. India, Coromandel [possible emendation].

Sphex argentifrons Lepeletier, 1845: 337. Lectotype ♂ (designated by Menke in Bohart & Menke 1975: 114): Java (Mus. Torino!).

Sphex plumifer Costa, 1864: 112. Philippines, Luzon (Mus. Naples).

Sphex umbrosus var. *nanulus* Strand, 1913: 83. Holotype ♀: Taiwan, Taihorin (DEI!).

Sphex umbrosus var. *fumosus* Kohl, 1890: 408. Japan (TMB).

Distribution. – Sri Lanka and India to Indochina and Japan; Malaysia, Indonesia, Philippines, Papua New Guinea and NE. Australia.

Note. – *Sphex unicolor* Fabricius, 1787, listed as a synonym of *argentatus* by Bohart & Menke (1975), was described from Spain where *argentatus* does not occur. Van der Vecht (1961) suggested that the name might refer to *S. fumicatus* Christ, 1791, but that species has never been reported from Spain either. The only Spanish species of *Sphex* that agrees with the description is *S. afer* Lepeletier. Alternatively, the locality may be incorrect.

Sphex diabolicus Smith

Sphex diabolicus Smith, 1858: 100. Lectotype ♀ (designated by Van der Vecht 1973): Sarawak (OUM!).

Sphex flammitrichus Strand, 1913: 83. Lectotype ♀ (present designation): Taiwan (DEI!).

Sphex umbrosus var. *aureopilosus* Berland, 1928: 330. Lectotype ♂ (designated by Menke in Bohart & Menke 1975): Ba-Cha, Tonkin (MNHN!).

Sphex fulvohirtus Bingham, 1890: 242. Holotype ♀: Sri Lanka, Pundalaya (BMNH!). Syn. n.

Types. – The lectotype of *Sphex flammitrichus* is a female labelled 'Kankau (Koshun), Formosa, H. Sauter, vii.1912', the paralectotypes are 3 males, labelled 'Korosan, Formosa, Sauter, xi.07' (all DEI!).

Distribution. – India and Sri Lanka to Malaysia, Indonesia (Sumatra and neighbouring islands, W. Java, Borneo, Sulawesi), Philippines.

Sphex finschii Kohl

(fig. 41)

Sphex finschii Kohl, 1890: 412. Lectotype ♂ (present designation): New Britain (ZMB!).

Distribution. – Indonesia (Ambon, Aru Islands, Irian Jaya), Papua New Guinea, Bismarck Islands, Solomon Islands, Australia.

Spbex madasummae Van der Vecht

Spbex caeruleus Guillo, 1841: 320. Holotype ♀: Borneo (MNHN!!) [non Reich, 1795].

Spbex maurus Smith, 1856: 255. Syntypes, ♀, ♂: Sulawesi (BMNH!!) [non Fabricius, 1787].

Spbex nigerrimus Costa, 1864: 112. Philippines, Luzon (Naples Museum?) [non Scopoli, 1763].

Spbex madasummae Van der Vecht, 1973: 345 [new name for *Spbex maurus* Smith].

Distribution. – Malaysia, Indonesia (not known from Nusa Tenggara); Philippines, Papua New Guinea.

Spbex sericeus Fabricius

(fig. 42)

Spbex aurulentus Fabricius, 1793: 201. – India, Tranquebar (location of type unknown) [non Fabricius, 1787].

Spbex sericeus Fabricius, 1804: 211. Lectotype ♀ (designated by Van der Vecht 1961): 'in maris pacifici Insulis' (Mus. Lund!).

Spbex fabricii Dahlbom, 1843: 27. ♀: India, Tranquebar (location of type unknown).

Spbex ferrugineus Lepeletier, 1845: 345. ♀: 'sans patrie, mais exotique' (MNHN?).

Spbex lineolus Lepeletier, 1845: 353. ♂: Java (MNHN?) [locality probably erroneous].

Spbex ferox Smith, 1862: 55. Syntypes, ♀, ♂: Ambon, Sulawesi (BMNH!!; OUM) [non Westwood, 1837].

Spbex lepeletierii Saussure, 1867: 40. Holotype ♀: Java (NMW!!) [locality probably erroneous].

Spbex godeffroyi Saussure, 1869: 57. ♀: Australia, Queensland, Cape York (Mus. Hamburg).

Spbex aurifex Smith, 1873: 460, pl. xlv, fig. 3. Holotype ♀: NW. Australia, Champion Bay (BMNH!!).

Spbex aurulentus var. *pallidehirtus* Kohl, 1890: 393. Syntypes ♂: New Guinea: Port Moresby; Ambon (NMW?).

Spbex rugosus Matsumura, 1912: 176, 53, fig. 8. ♀: Taiwan: Horisha, Koshun.

Spbex sericeus ferocior Van der Vecht & Krombein, 1955: 40 [new name for *Spbex ferox* Smith].

Spbex sericeus nigrescens Van der Vecht & Krombein, 1955: 39. Holotype ♀: Philippines, Luzon, Los Baños (USNM).

Spbex sericeus stueberi Van der Vecht & Krombein, 1955: 42. Holotype ♀: Indonesia, Irian Jaya, Jayapura (RMNH!!).

Spbex sericeus wegneri Van der Vecht & Krombein, 1955: 39. Holotype ♂: Indonesia, Kalimantan, Samarinda, Mura Kaman (RMNH!!).

Distribution. – India and Sri Lanka to China and Indochina, Malaysia, Indonesia, Philippines, Papua New Guinea, N. Australia.

Note. – This species occurs in many colour-forms, which are largely allopatric. Van der Vecht and Krombein (1955) recognized eight subspecies.

Group of *Spbex resplendens* Smith

Diagnosis

Body length ♂ 17–24 mm, ♀ 20–33 mm. Mandible of both female and male bidentate; antenna of male without placoids; scutellum of female flat or very weakly convex, conspicuously shiny, of male convex, medially not or hardly impressed; claw teeth small, perpendicular to claw.

Species included

Species treated. – *S. brachystomus* Kohl, *confrater* Kohl, *dorycus* Guérin-Méneville, *mimulus* Turner, *muticus* Kohl, *resplendens* Kohl, *solomon* sp. n., *wilsoni* sp. n.

Other included species. – *S. fumipennis* Smith, *S. gilberti* Turner, *S. luctuosus* Smith (all from Australia), and *S. antennatus* Smith stat. n. (from New Caledonia, New Hebrides and Loyalty Islands; listed as a subspecies of *S. fumipennis* by Bohart & Menke 1976).

Key to species

- Metasoma partly red (sometimes only part of posterior tergites) 2
 - Metasoma entirely black 4
- Pilosity of mesosoma white; 8th sternite of male with narrow apical process; Australia, New Guinea *mimulus* Turner
 - Pilosity of mesosoma dorsally yellow to black, ventrally brownish to black; 8th sternite of male triangular, without process 3
- Metasoma except petiole entirely red; pilosity of mesosoma dorsally yellow to brownish; petiole of female longer than wide; gonostyles of male without inner lobe; New Guinea *dorycus* Guérin-Méneville
 - Metasoma with only posterior tergites and sternites red; pilosity of mesosoma black; petiole of female as long as wide; gonostyles of male ventrally with flat, almost circular inner lobe (fig. 56); Solomon and Bismarck Islands *confrater* Kohl
- Mesonotum densely covered with silvery or golden tomentum, completely obscuring sculpture 5
 - Mesonotum without or with sparse tomentum, sculpture visible throughout 6
- Tomentum golden; wings yellowish, apical margins infuscate; New Guinea *wilsoni* sp. n.
 - Tomentum silvery; wings dark brown, with violaceous effulgence; New Guinea, Bismarck Islands *brachystomus* Kohl
- Females 7
- Males 9
- Mandibles long, strongly curved (fig. 13),

when closed reaching beyond base of opposite mandible; apical margin of clypeus strongly arcuate; median carina of labrum projecting into a small apical tooth; Buru, Ambon *muticus* Kohl

- Mandibles short, moderately curved (fig. 15), when closed not reaching base of opposite mandible; anterior margin of clypeus weakly arcuate; median carina of labrum not projecting apically 8
- 8. Interocular distance at vertex longer than combined lengths of flagellomeres II + III; metanotum without silvery tomentum; Moluccas, New Guinea, Philippines, Australia *resplendens* Kohl
- Interocular distance at vertex equal to combined lengths of flagellomeres II + III; metanotum densely covered with silvery tomentum; Solomon Islands *solomon* sp. n.
- 9. Mandibles with basal half straight, sharply curved inward distally (fig. 14); petiole in dorsal view more than 2 times as long as wide; gonostyles not emarginate, the apex simple; Buru, Ambon *muticus* Kohl
- Mandibles smoothly curved, approximately a quarter-circle (fig. 16); petiole in dorsal view less than 2 times as long as wide; gonostyles dorsally emarginate, the apex produced into tooth pointing upward (fig. 58) 10
- 10. Pilosity of head and mesosoma dark brown to black; wings dark brown; Philippines, Moluccas, New Guinea, Australia *resplendens* Kohl
- Pilosity of head and mesosoma yellowish, partly dark brown on head and mesosomal dorsum; wings brownish hyaline; Solomon Islands *solomon* sp. n.

Sphecx brachystomus Kohl

Sphecx brachystomus Kohl, 1890: 415. Syntypes ♀ ♂: New Britain (NMW!).

Distribution. – Papua New Guinea, Bismarck Islands (New Ireland, New Britain).

Sphecx confrater Kohl

(fig. 56)

Sphecx confrater Kohl, 1890: 414. Syntypes ♀: New Britain ('Mus. Hammon').

? *Sphecx confrater* var. *sieberti* Strand, 1910: 46. Syntypes ♀: Java, Batavia (location of types unknown).

Distribution. – Solomon Islands (Kolombangara, Guadalcanal), Papua New Guinea, Bismarck Islands (New Britain, New Ireland).

Note. – Judging on the type-locality, it seems very unlikely that *sieberti* Strand is indeed a variety of *confrater*, but it is not clear from the description to which other species it might pertain.

Sphecx dorycus Guérin-Ménéville

Sphecx dorycus Guérin-Ménéville, 1838: 262. Holotype ♀: New Guinea, Manokwari ('Dory') (MCG).

Sphecx errabundus Kohl, 1898: 338. Holotype ♀: Indonesia, Waigeo ('Waigiu') (TMB!).

Distribution. – Indonesia (Waigeo, Irian Jaya), Papua New Guinea.

Note. – The synonymy of this species was discussed by Van der Vecht (1973).

Sphecx mimulus Turner

Sphecx mimulus Turner, 1910b: 419. Holotype ♀: Australia, Queensland, Cairns (BMNH!).

Distribution. – Australia (Queensland), S. Papua New Guinea.

Sphecx muticus Kohl

(figs. 13-14, 57)

Sphecx muticus Kohl, 1885: 199. Lectotype ♂ (designated by Van der Vecht 1973): Indonesia, Ambon (NMW!).

Distribution. – Indonesia (Buru, Ambon).

Sphecx resplendens Kohl

Sphecx nitidiventris Smith, 1859: 158. Holotype ♀: Indonesia, Buru (OUM!) [non Spinola, 1851].

Sphecx graciosus Smith, 1859: 158. Holotype ♂: Indonesia, Aru Islands (OUM!) [non Smith, 1856].

Sphecx resplendens Kohl, 1885: 200 [new name for *S. nitidiventris* Smith].

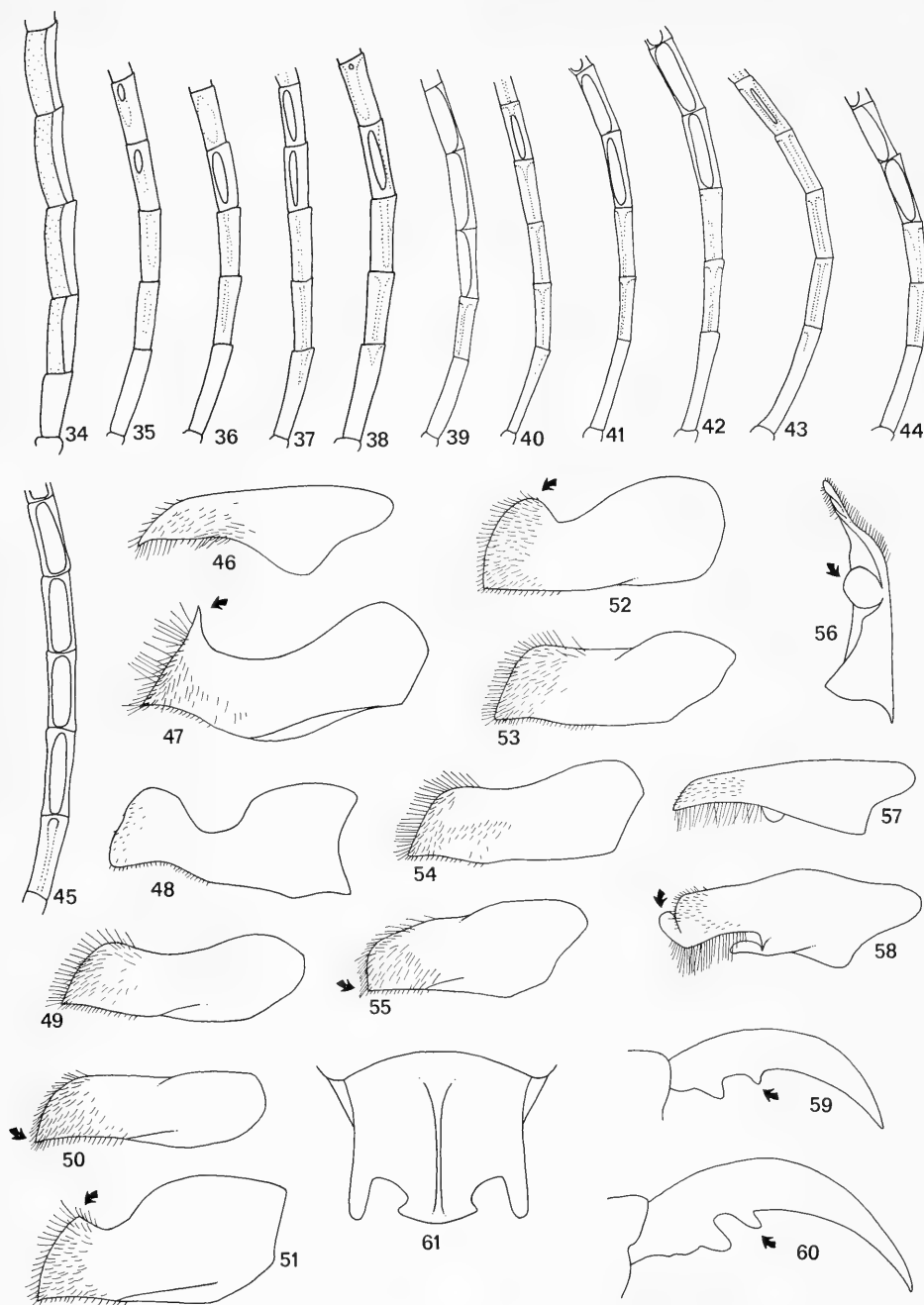
Sphecx gratiosissimus Dalla Torre, 1897: 424 [new name for *S. graciosus* Smith, 1859].

Sphecx wallacei Turner, 1908: 467 [new name for *S. nitidiventris* Smith].

Sphecx lanceiventris Vachal, 1908: 23 [new name for *S. nitidiventris* Smith].

Sphecx mertonii Strand, 1911: 231. Holotype ♀: Indonesia, Aru Islands, Kobroör, Seltutti (Mus. Senckenberg!).

Distribution. – Philippines (Negros, Luzon); Indonesia (Aru Islands, Key Islands, Bacan, Ambon, Irian Jaya); Papua New Guinea, Australia (Queensland). A few specimens from Bangka in the RMNH are probably incorrectly labelled.



Figs. 34-61. *Isodontia* and *Sphex*. 34-45, proximal flagellomeres of ♂. – 34, *I. ochroptera*; 35, *I. elsei*; 36, *I. jaculator*; 37, *I. prasinia*; 38, *I. sepicola*; 39, *S. alacer*; 40, *S. argentatus*; 41, *S. finschi*; 42, *S. sericeus*; 43, *S. rex*; 44, *S. subtruncatus*; 45, *S. walsbae*. 46-58, Gonostyle of ♂, 46-55 + 57-58, lateral view, 56, ventral view. – 46, *I. pilipes*; 47, *I. capillata*; 48, *I. cestra*; 49, *I. delicata*; 50, *I. diodon*; 51, *I. egeus*; 52, *I. immaculata*; 53, *I. papua*; 54, *I. permutans*; 55, *I. severini*; 56, *S. confrater*; 57, *S. muticus*; 58, *S. solomon*. 59-60, tarsal claw. 59, *S. solomon*, ♀; 60, *S. subtruncatus*, ♀. 61, *S. rex*, ♂, eighth sternite.

***Sphex solomon* sp. n.**
(figs. 15-16, 58-59)

Type material. – Holotype ♂, Solomon Islands, Guadalcanal Is., Lunga, 2.xii.1934, H. T. Pagden (RMNH). – Paratypes: Solomon Islands: Tulagi (3 ♀), Guadalcanal, Lunga (1 ♀ 1 ♂), Ganonga (1 ♀ 5 ♂), Nygela (1 ♀), all H. T. Pagden (RMNH); Guadalcanal, Kukum, P. Greenslade (1 ♀, BMNH); Isabel, Tatamba (1 ♀, Australian National Insect Collection, Canberra; 1 ♀, RMNH); Bougainville, Buin, G. Daniels (1 ♀, Australian Museum, Sydney); Guadalcanal, Lunga River Bridge, J. Schenk (1 ♂, Los Angeles County Museum); Guadalcanal, Kukum, E. S. Brown (1 ♂ 7 ♀, BMNH, 2 ♀, RMNH).

Diagnosis

Similar to *resplendens* and *brachystomus*, with which *solomon* shares relatively short and weakly curved mandibles, and an apical lobe on the male gonostyle. It differs from these species in vestiture: the silvery tomentum of the mesosoma is restricted to the pro- and metanotum, particularly conspicuous on the latter, in male, the pilosity of head and mesosoma is basically pale. Structural features are: in female, IOV equals flagellomere 2 + 3 (longer in *resplendens* and *brachystomus*); in male the apical lobe of the gonostyle is broad and rounded (narrow, pointed in the other species).

Description

Female. – Body length 20-25 mm; length of forewing 15.0-18.5 mm. Black, metasoma with fine greenish metallic shine. Wings brown. Pilosity of head and mesosoma dark brown; facial tomentum brownish to silvery; mesosoma with conspicuous silvery tomentum on metanotum and sometimes on pronotum. Clypeus 0.8 times as long as IOC, with weak median keel on dorsal half, apical margin slightly raised, with a pair of short teeth medially; IOV 0.75 times IOC; labrum with median carina, which does not project apically; relative lengths of flagellomeres I-III 1 : 0.6 : 0.6. Mesopleuron sparsely finely punctate, interspaces punctulate, shiny; mesoscutum densely, rather coarsely punctate, punctures 0.5-1 diameter apart, interspaces smooth, shiny; scutellum slightly convex, sparsely finely punctate, shiny; propodeum coriaceous, dull. Fore basitarsus with 8 rake spines, median spines 2 times tarsal width, apical spine as long as second tarsomere. Petiole 0.3 times as long as hind basitarsus, in dorsal view hardly longer than wide.

Male. – Body length 19-24 mm; length of forewing 13.5-17.0 mm. Like the female except for the following. Wings brownish hyaline, apical margins infuscate. Facial tomentum silvery; pilosity of head and mesosoma basically pale, more or less mixed with dark hairs or entirely dark on vertex, temples and mesosomal dorsum. Clypeus 0.95 times as long

as IOC, apical margin untoothed, medially depressed; IOV 0.85 times IOC; labrum ecarinate; scutellum convex, faintly impressed along midline. Apical margins of second to seventh sternite with row of black setae; eighth sternite apically produced into a tooth, distal third medially keeled; gonostyle apically with short lobe pointing upward, ventrally in the middle with almost circular lobe pointing inward.

Etymology

Solomon is a noun in apposition, referring to the type locality.

***Sphex wilsoni* sp. n.**

Type material. – Holotype ♀, Papua New Guinea, Huon Peninsula, Mongi-Mape Watersheds, Nganduo to Yunzain, 1000-1500 m, 56.iv.1955, E. O. Wilson (MCZ).

Diagnosis

Immediately separated from other species of the *resplendens*-group by the conspicuous golden tomentum on head and thorax, and the yellow wings. Structurally, *wilsoni* is similar to *confrater*, *mimulus*, *dorycus* and *muticus*, with which it shares the long, strongly curved mandibles.

Description

Female. – Body length 25 mm; length of forewing 19 mm. Black; metasoma with fine metallic shine. Wings yellow, apical margins infuscate. Pilosity of head and mesosoma dark brown; head, pro-, meso- and metanotum with dense golden tomentum, completely obscuring the sculpture of these parts. Clypeus 0.75 times as long as IOC, with weak median carina dorsally; apical margin slightly raised, with a pair of short teeth medially; IOV 0.75 times IOC; labrum with median carina, projecting apically into a short tooth; mandibles long, strongly curved, when closed reaching beyond each other's bases (cf. fig. 13); relative length of flagellomeres I-III 1 : 0.6 : 0.65. Mesopleuron sparsely finely punctate, interspaces weakly punctulate; mesonotum apparently (obscured by vestiture) densely finely punctate, shiny; propodeum finely coriaceous, dull; fore basitarsus with 9 rake spines, median spines 1.4 times tarsal width, apical spine shorter than second tarsomere. Petiole 0.25 times as long as hind basitarsus, in dorsal view hardly longer than wide.

Etymology

Wilsoni is a noun in the genitive case, referring to E.O. Wilson, collector of the only known specimen of this species.

Group of *Spbex subtruncatus* Dahlbom

Diagnosis

Body length ♂ 16-28 mm, ♀ 15-36 mm. Mandible of both male and female bidentate; antenna of male with placoid(s); scutellum convex, medially impressed; metanotum simple; claw teeth large, at sharp angle to claw.

Species included

Species treated. – *S. cognatus* Smith, *formosellus* Van der Vecht, *praedator* Smith, *rex* sp. n., *staudingeri* Gribodo, *subtruncatus* Dahlbom, *walshae* sp. n.

Other included species. – *S. obscurus* (Fabricius) (Sri Lanka to Thailand, *abasverus* Kohl, *semiforsulatus* Van der Vecht, *vestitus* Smith, *ermineus* Kohl, and *bilobatus* Kohl (all Australian).

Note. – This is obviously a heterogeneous assemblage. The species are grouped together only on basis of the lack of specialized features defining the other groups. It is undoubtedly paraphyletic, but I have not been able to find an adequate way of splitting it up.

Key to species

1. Propodeum with dense golden or silvery tomentum, completely obscuring sculpture.... 2
- Propodeum at most with sparse golden or silvery tomentum, leaving sculpture easily visible 3
2. Large species: wing length 26-27 mm; legs largely reddish; New Guinea *rex* sp. n.
- Medium-sized species: wing length 13-19 mm; legs black; Moluccas, New Guinea, Bismarck and Solomon Islands, Australia *cognatus* Smith
3. Female: outer side of mid tibia only with normal, straight spines apically; male: apical margin of clypeus straight or slightly concave, without median lobe (fig. 17) 4
- Female: outer side of mid tibia with stout, curved spine apically (fig. 64); male: apical margin of clypeus with short median lobe (fig. 18) 6
4. Wings strongly yellowish to dark brown with violaceous effulgence; India to Moluccas, Philippines *praedator* Smith
- Wings basically clear, at most slightly yellowish and apically infuscate 5
5. Pilosity of head and mesosoma dense, yellowish brown; face and mesoscutum with dense brownish tomentum obscuring the sculpture; legs reddish; medium-sized species, wing length 19-20 mm; New Guinea *staudingeri* Gribodo
- Pilosity of head and mesosoma white to pale

yellow; mesoscutum without dense tomentum, sculpture easily visible; legs black; small species, wing length 10.5-13.5 mm; Sumba, Timor, W. Australia *formosellus* Van der Vecht

6. Wings dark brown with bluish effulgence, legs dark; female: sixth tergite with pygidium (fig. 65); male: 3rd to 7th flagellomere with broad placoids (fig. 45); Burma to Sumatra, Borneo *walshae* sp. n.
- Colour of wings and legs variable; female: sixth tergite without pygidium; male: 3rd flagellomere rarely with placoid (only in specimens from Philippines and Java) (fig. 44); Sri Lanka to Philippines and Timor *subtruncatus* Dahlbom

Spbex cognatus Smith

Spbex cognatus Smith, 1856: 248. Holotype ♀: Australia (BMNH!).

Spbex amator Smith, 1856: 246. Holotype ♂: Australia (OUM!).

Spbex formosus Smith, 1856: 254. Holotype ♀: Indonesia, Seram (BMNH!).

Spbex opulentus Smith, 1856: 250. Holotype ♂: Australia, Richmond River (BMNH!).

Distribution. – Indonesia (Maluku, Irian Jaya), Papua New Guinea, Bismarck Islands, Solomon Islands, Admiralty Islands, Australia.

Note. – Specimens from the North Moluccas (Halmahera etc.) differ from the remaining populations in having silvery tomentum with a faint golden tinge, in particular on the propodeum.

Spbex formosellus Van der Vecht

Spbex formosellus Van der Vecht, 1957: 366. Holotype ♀: Timor (RMNH!).

Distribution. – Indonesia (Timor, Sumba), W. Australia.

Spbex praedator Smith

(fig. 17)

Spbex praedator Smith, 1858: 14. Holotype ♂: Indonesia, Sulawesi (OUM!).

Spbex tyrannicus Smith, 1860: 122. ♀: Indonesia, Bacan (type lost, Van der Vecht 1973).

Spbex luteipennis Mocsary, 1883: 33. Lectotype ♀ (designated by Van der Vecht 1973): Indonesia, Ambon (TMB!).

Spbex nigripes var. *calopterus* Kohl, 1890: 168, 422 [as var. 5]. ♂: Indonesia, Sulawesi (NMW).

Spbex nigripes var. *koblianus* Strand, 1913: 81 [new name for *S. nigripes* var. *calopterus* Kohl].

Spbex nigripes var. *celebesianus* Strand, 1913: 81. ♀, ♂:

Indonesia, Sulawesi (NMW) [name for *S. nigripes* var. 2 of Kohl (1890)].

Sphex nigripes var. *melanopodus* Strand, 1915: 89. Lectotype ♀ (designated by Van der Vecht 1973): Sri Lanka, Nalanda (NMW!).

Distribution. – India and Sri Lanka to China and Malaysia, Indonesia (Sumatra, Sangehe Islands, Java, Sulawesi, Moluccas), Philippines.

***Sphex rex* sp. n.**
(figs. 43, 61–62)

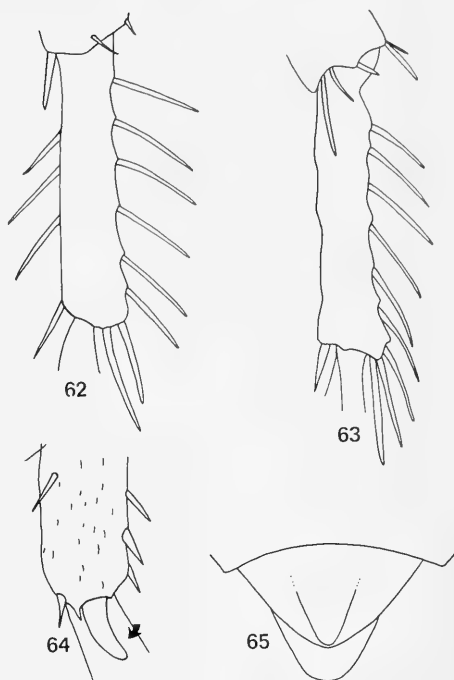
Type material. – Holotype ♀, Papua New Guinea, Milne Bay, KBMission, 5.iii.1944, K.V. Krombein (USNM). – Paratype: Indonesia, Irian Jaya, Ifar, 350 m, iii.1957, J. v.d. Assem (1 ♂, RMNH).

Diagnosis

This species is immediately recognized by its large size (body length 35 mm), reddish legs and dense golden tomentum on most part of mesosoma. In these respects it is similar only to *S. basilicus* from Australia, from which it differs as follows: petiole short, 0.35 times as long as hind basitarsus (0.5 in *basilicus*); 7th sternite of male with proximal transverse depression, 8th sternite trilobate (bilobate in *basilicus*); anterior femora of female ventrally covered with tomentum (with sparse erect pilosity in *basilicus*).

Description

Female. – Body length 36 mm, length of forewing 26 mm. Black, the following parts reddish: mandibles except base and apex, femora except basal half, tibiae, tarsi, tegulae except medially, sixth metasomal segment. Wings almost clear, apically infusate. Pilosity yellow, on vertex and mesoscutal disc infusate; head and mesosoma with conspicuous dense golden tomentum, completely obscuring sculpture of metanotum and propodeum, tomentum on anterior part of mesoscutal disc and scutellar disc dark brown; fore femora ventrally with tomentum and pilosity. Clypeus 0.85 times as long as IOC, with blunt median carina on dorsal half, apical margin with short median lobe; IOV 0.85 times IOC; labrum with median carina, which projects apically into a weak tooth; relative lengths of flagellomeres I–III 1 : 0.6 : 0.6. Mesosoma microsculptured, punctulate to punctulate-reticulate to shagreened (obscured by vestiture almost throughout); scutellum with median longitudinal impression; fore metatarsus with 8 rake spines, median spines 1.5 times metatarsal width, apical spine as long as second tarsomere; mid tibia with oblique, slightly curved spine apically. Petiole 0.35 times as long as hind basitarsus; sixth tergite without pygidium.



Figs. 62–65. *Sphex*. 62, *S. rex*, ♀, fore basitarsus; 63–65, *S. walsbae*, ♀. 63, fore basitarsus; 64, distal part of mid tibia, outer side; 65, sixth tergite.

Male. – Body length 35 mm, length of forewing 27 mm. Like the female except for the following. Mandibles black, mid and hind femora nearly entirely black; 7th metasomal segment and 8th sternite reddish. First tergite and sides of 6th and 7th with conspicuous yellow pilosity. Clypeus 0.95 times as long as IOC; IOV 0.9 times IOC; labrum ecarinate; relative lengths of flagellomeres I–III 1 : 0.65 : 0.65, 5th flagellomere with narrow concave placoid; sixth sternite apically shallowly emarginate, seventh sternite proximally transversely depressed, 8th sternite trilobate, middle lobe curved upward.

Etymology

Rex is a noun in apposition, from Latin *rex* = king.

***Sphex staudingeri* Gribodo**

Sphex staudingeri Gribodo, 1894: 3. Holotype ♂: New Guinea (MCG!).

Distribution. – New Guinea.

***Sphex subtruncatus* Dahlbom**

(figs. 44, 60)

Sphex subtruncatus Dahlbom, 1843: 25. ♀: 'Africa' (Museum Lund!) [probably from NE. India, see Van der Vecht (1973)].

Sphex nigripes Smith, 1856: 254. Syntypes ♀: China: Shanghai (BMNH!), Sumatra [non Fabricius, 1793].

Sphex siamensis Taschenberg, 1869: 413. ♀: 'Siam' (Mus. Univ. Halle!) [probably from the Philippines, according to Van der Vecht (notes)].

Sphex erythropodus Cameron, 1889: 108. Syntypes ♀: India (Mus. Calcutta).

Sphex sulciscuta Gribodo, 1894: 2. Holotype ♀: Philippines, Mindoro (MCG!).

Sphex nigripes var. *tsingtauensis* Strand, 1916: 81A (11): 107. Holotype ♂: China, Tsingtau [Qingdao] (DEI!).

Sphex subtruncatus coraxus Van der Vecht, 1957: 365. Holotype ♀: Indonesia, Sumba, Pogobina (NMB!).

Sphex subtruncatus orius Van der Vecht, 1957: 366. Holotype ♂: Indonesia, Flores, Rana Mese (NMB!).

Sphex subtruncatus xuthus Van der Vecht, 1957: 364. Holotype ♂: Indonesia, Sumba, Bondo Kodi (NMB!).

Sphex subtruncatus krombeini Van der Vecht in Krombein, 1984: 28. Holotype ♀: Sri Lanka, Kanneliya Jungle (USNM!).

Distribution. – Sri Lanka and India to China and Malaysia, Indonesia (Sumatra, Bangka, Java, Kalimantan, Lombok, Flores, Sumba, Timor), Philippines.

Note. – *S. subtruncatus* exists in a number of geographic forms, which differ in colour (legs black to reddish, wings dark brown to clear), as well as in the number of placoids on the male flagellum.

***Sphex walsbae* sp. n.**

(figs. 18, 45, 63–65)

Type material. – Holotype ♀, Indonesia, S. Sumatra, 250 m, Bengkulu, Muara Tenam, 16–23.vii.1935, M. E. Walsh (RMNH). – Paratypes: India: Sikkim, Ari to Gnatong, 7–2500 ft, iv.1894, Bingham (1 ♀, USNM). Burma: Tenasserim, Ihaungyin Valley, v.1891, Bingham (1 ♀, BMNH). Malaysia: Malay peninsula, Kedah Peak, 3000–3500 ft, 15.iii.1928, H. M. Pendlebury (1 ♀, BMNH); Sarawak, C. J. Brooks (1 ♀, BMNH); Sabah, Sandakan, Baker (2 ♀, USNM); Sabah, 19 km N. of Kalabakan, 19.xi.1962, Y. Hirashima (1 ♀, BPBM); North Borneo, Fröhstorfer (1 ♀, TMB). Indonesia. Sumatra: Anei kloof, 500 m, E. Jacobson (3 ♀, RMNH); Bengkulu, 50 m, 10–18.v.1935, M. E. Walsh (1 ♀, RMNH); Bengkulu, Bukit Item, 650 m, 11–15.vi.1935, M. E. Walsh (1 ♀, RMNH); Bengkulu, Tandjong Sakti, 1–10.vi.1935, M. E. Walsh (2 ♂ 1 ♀, RMNH); Lubuk Sikaping, 450 m, L. Lundeshagen (1 ♀, RMNH), Aur Kemanis, E. Jacobson (1 ♀, RMNH); no locality (1 ♀, Zoologische Staatssammlung, München). Kalimantan: Ketapan, v.1937, M. E. Walsh (2 ♀, RMNH); Sampagan, 0 m, 1927, M. E. Walsh (1 ♂, RMNH); South coast (1 ♀, RMNH); Kembang Djangut, 75 m, 24–30.xi.1956, A.M.R. Wegner (5 ♀, RMNH); no locality, Muller (1 ♂ 5 ♀, RMNH). 'Ind. or.' (1 ♀, RMNH).

Diagnosis

This species is similar to other large, dark-winged, dark-legged forms: the representative of *S. subtruncatus* in the Philippines and the representative of *S. praedator* in the Moluccas (apart from species belonging in other groups). As these forms are allopatric, *S. walsbae* may be separated from sympatric forms on the basis of the dark brown wings with violaceous effulgence. Unlike *S. praedator*, *S. walsbae* has a stout curved spine at the outer end of the female mid tibia, and the male clypeus has a median apical lobe. In these respects *S. walsbae* is similar to *S. subtruncatus*, from which it differs in having a pygidial plate in the female, and placoids on third to 7th flagellomere in the male (variable in *S. subtruncatus*, the mentioned condition occurring in specimens from the Philippines and Java).

Description

Female. – Body length 23–28 mm, length of forewing 17–20 mm. Black. Wings dark brown with violaceous effulgence. Pilosity of head and mesosoma black; clypeus and frons with sparse silvery tomentum, mesosoma with sparse, inconspicuous dark brown tomentum; fore femora ventrally with sparse erect hairs, no tomentum. Clypeus 0.8 times as long as IOC, without median carina, apical margin slightly raised and with a pair of short teeth medially; IOV 0.8 times IOC; labrum with median carina, which projects apically into a tooth; relative lengths of flagellomeres I–III 1 : 0.7 : 0.75. Mesosoma microsculptured: punctulate-reticulate to shagreened, mesonotum and mesopleuron largely shallowly punctate, punctures 1–2 diameters apart; propodeum finely rugose; scutellum with median longitudinal impression; fore basitarsus with 9–10 rake spines, median spines 1.5 times tarsal width, apical spine as long as second tarsomere; apex of mid tibia with stout curved spine. Petiole 0.4 times as long as hind metatarsus; sixth tergite with pygidium.

Male. – Body length 21–24 mm; length of forewing 16–18 mm. Like the female except for the following. Clypeus 0.9 times as long as IOC, apical margin with short, depressed median lobe; IOV 0.85 times IOC; labrum ecarinate; length of flagellomeres I–III 1 : 0.75 : 0.75, third to seventh flagellomere with broad, flat placoid. Seventh sternite weakly emarginate; eighth sternite triangular.

Etymology

Walsbae is a noun in genitive case, referring to Mrs. M. E. Walsh, collector of a substantial part of the type series.

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CARYOCOLUM DELPHINATELLA (CONSTANT) SP. REV.,
A SENIOR SYNONYM OF *C. FIORII* (KLIMESCH)
(LEPIDOPTERA: GELECHIIDAE)

Huemer, P., 1991. *Caryocolum delphinatella* (Constant) sp. rev., a senior synonym of *C. fiorii* (Klimesch) (Lepidoptera: Gelechiidae). – Tijdschrift voor Entomologie 134: 31-34, figs. 1-7. [ISSN 0040-7496]. Published 1 July 1991.

Caryocolum delphinatella (Constant) is recognized as good species and revoked from synonymy with *C. interalbicella* (Herrich-Schäffer). The female genitalia are described and figured and data on biology are given. *C. fiorii* (Klimesch) is synonymised with *C. delphinatella*.

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Key words. – Gelechiidae, *Caryocolum*, synonymy.

In 1890 the well-known French lepidopterist A. Constant described *Lita delphinatella* from a single female collected in July in the Alpes du Dauphiné. Klimesch (1954) in his revision of European species of the former genus *Lita* feeding on Caryophyllaceae, queried *delphinatella* as a synonym of *Caryocolum interalbicella* (Herrich-Schäffer). This synonymisation was accepted by the present author (Huemer 1988) although *delphinatella* was treated as a separate species in the French list (Leraut 1980). *C. fiorii* was described from five males collected in the Abruzzi (Klimesch 1953). Later the species was also recorded from the Swiss and French Alps.

When re-evaluating the original description of *delphinatella*, including the colour plate depicting the holotype, it became clear that this species is not a synonym of *interalbicella* but conspecific with *fiorii*. This assumption is further supported by rich material, including two females, collected in the south-western Alps in July 1990.

Caryocolum delphinatella (Constant) sp. rev.

Lita delphinatella Constant, 1890a (May 28): 6, pl. 1, fig. 2 [moth in colour]. Holotype ♀, France: Alpes du Dauphiné, vii [not traced].

Lita delphinatella Constant; Meess 1910: 370.

Phthorimaea delphinatella (Constant); Meyrick 1925: 95; Gaede 1937: 254; Lhomme [1946]: 632.

Caryocolum delphinatella (Constant); Leraut 1980: 79.

Gnorimoschema fiorii Klimesch, 1953: 277, figs 23, 24.

Lectotype ♂ (Designated by Huemer 1988: 481), Italy:

Abruzzan, Gran Sasso, 25.vii.1935 (Fiori) (coll. Klimesch, Linz) [examined]. Syn. n.

Caryocolum fiorii (Klimesch); Huemer 1988: 480.

Description

Adult (Figs 1, 3-5). – Fore wing length ♂ 7.0-7.5 mm, ♀ 6.5-7.0 mm. Head white; Labial palpus white, third segment mottled with dark brown. Thorax white, tegulae dark brown basally. Fore wing dark brown, mottled with light brown; white transverse fasciae at one-fifth and one-half, medially narrowed and often reduced towards costa; fasciae fused and mottled with light brown dorsally; separate white subcostal spot at about two-fifth always well developed; white costal and tornal spots at four-quarters variable in extension, separate or fused to fascia; fringes whitish with dark brown basal line. Hind wing light grey.

Male genitalia (Huemer 1988: Fig. 122).

Female genitalia (Figs 6, 7). – Apophyses posteriores 1.60 mm, apophyses anteriores 0.43 mm; eighth segment without processes; ostium bursae surrounded by folds; antrum short, funnel-shaped, posteriorly fused with pair of short lateral sclerotizations of ductus bursae which are level with the tip of the apophyses anteriores; corpus bursae pyriform with long, hook-shaped signum.

Biology

The immature stages are still unknown. According to personal observations in France the larvae probably feed on *Minuartia* sp. and *Silene* sp. (Ca-



1



2



3



4



5

Figs. 1-5. *Caryocolum* spp. – 1, *C. delphinatella*, original figure by Constant; 2, *C. interalbicella*; 3, *C. delphinatella* (*fiorii* lectotype); 4, *C. delphinatella* ♀; 5, *C. delphinatella* ♂.

ryophyllaceae) around which the adults have been collected in numbers in July and early August; most specimens were attracted to artificial light sources. The females examined were both collected during day time resting on rocks. *C. delphinatella* is an alpine species which occurs from about 1600 to 2500 m.

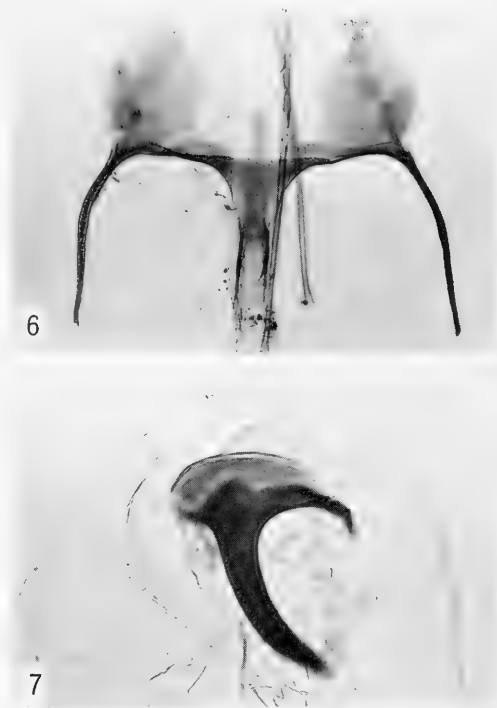
Distribution

Only known from the Abruzzi and the south-western Alps (Alpes Maritimes, Alpes de Haute Provence, Hautes Alpes, Isère (Dauphiné), Walliser Alpen, Alpi Cozie); according to Lhomme [1946] also in the Pyrénées (Haute-Garonne).

Remarks

Despite the efforts of several lepidopterists the holotype of *delphinatella* could not be traced in MNHN Paris or any other institution; however, Constant's original description and colour illustration, the latter reproduced here in monochrome (Fig. 1), leave no doubt about the identity of this species. It is well characterized by the pure white head and thorax as emphasised by Constant, and the white subcostal forewing spot at two-fifths (Figs 1,3-5). The synonymisation with *Caryocolum interalbicella* is certainly incorrect as this species has a whitish to cream head and tegulae and a dark brown thorax (Fig. 2). The few French *Caryocolum*-species with white colour of head and thorax differ from *delphinatella*: *C. saginella* (Zeller) is distinctly smaller (4.0-5.0 mm); *C. cauligenella* (Schmid) has a creamy rather than pure white head and thorax and also broader fore wings without the costal spot present in *delphinatella*; French specimens of *C. peregrinella* (Herrich-Schäffer) are characterized by the larger size (7.5-9.0 mm), broader fore wings and extended white markings of the fore wing without separate subcostal spot. *C. leucothoracellum* (Klimesch) has different forewing markings with white subcostal streak and a medial spot. *C. fiorii* perfectly matches *delphinatella* and is here placed as a junior subjective synonym. *C. fiorii* was recently recorded as new to France (Huemer 1989) because the true identity of *delphinatella*, at that time still treated as synonym of *interalbicella*, was not recognized.

The female genitalia of *delphinatella* are similar to those of other species of the *trauniella*-group. The antrum is distinctly longer than in *peregrinella* (Herrich-Schäffer) and *trauniella* (Zeller). The lateral sclerotizations of the ductus bursae are level with the tip of the apophyses anteriores in *delphinatella* whereas in other species of the group they are at most half that length. The differences in the male genitalia have been discussed previously (Huemer 1988).



Figs. 6-7. *Caryocolum delphinatella*, female genitalia. – 6, eighth segment; 7, signum ($\times 2$ magnification of eighth segment).

Material examined (additional to that previously recorded (Huemer 1988, 1989). – Italy: 4 ♂, Abruzzan, Prov. Rieti, Terminillo-Paß, 18-2000 m, 5-6.viii.1970, leg. Groß; 2 ♂, P. d. Fargno, ob. Bolognola, Mti. Sibillini, 16-1700 m, 14.viii.1970, leg. Groß (Löbbecke Museum, Düsseldorf); 1 ♂, Prov. Torino, Alpi Cozie, Colle delle Finestre, 2150 m, 27.vii.1990, leg. Huemer & Tarmann. France: 39 ♂, 1 ♀, Dep. Alpes-Maritimes, Marguareis W-Hang, Navela, 2100-2200 m, 21-23.vii.1990, leg. Huemer & Tarmann; 22 ♂, 1 ♀, Dep. Alpes-de-Haute-Provence, SW Castel de Restfond, Roche Chevalière, 2480 m, 25.vii.1990, leg. Huemer & Tarmann; 10 ♂, Dep. Alpes-de-Haute-Provence, SW Castel de Restfond, Set. de Caire Brun N-Flanke, 2420 m, 25.vii.1990, leg. Huemer & Tarmann (Tiroler Landesmuseum Ferdinandeum, Innsbruck).

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CUTICULAR BLADES AND OTHER STRUCTURES OF *DIAPREPOCORIS* KIRKALDY AND *STENOCORIXA* HORVATH (HETEROPTERA: CORIXIDAE)

Lansbury, I., 1991. Cuticular blades and other structures of *Diaprepocoris* Kirkaldy and *Stenocorixa* Horvath (Heteroptera: Corixidae). – Tijdschrift voor Entomologie 134: 35-46, figs. 1-27. [ISSN 0040-7496]. Published 1 July 1991.

Diaprepocoris Kirkaldy and *Stenocorixa* Horvath possess cuticular blades and modified swimming hairs on their hind tibiae and tarsi which resemble those of gyrids (Coleoptera: Gyridae). These have not previously been recorded in the Corixidae. Unusual macrotrichia are also present on the clavus and corium of all known species of both genera. The unique characters of these two genera support their separate subfamily placements. I. Lansbury, Hope Entomological Collections, University Museum, Oxford, OX1 3 PW, U.K.

Keywords. – Australia, Africa, Cuticular blades, modified swimming hairs, respiration, Corixidae.

A study of the Australasian *Diaprepocoris* has revealed the presence of cuticular blades and modified swimming hairs on the hind tibiae and tarsi. These structures have not previously been reported in the Corixidae. A survey of the corixid genera has shown that a similar combination of cuticular blades and modified swimming hairs are also present in the genus *Stenocorixa* which is restricted to tropical Africa. The cuticular blades and associated specialised swimming hairs are described and their probable function discussed in relation to the nektonic (submerged) swimming strategies and respiration in both subfamilies.

The double hair pile layer on the forewings of *Diaprepocoris* is figured and a dual function suggested for the hair pile. *Diaprepocoris* is compared with *Stenocorixa*, the later apparently having smooth forewings. The relationship between the gas stores of *Diaprepocoris* and the specialised swimming hairs of the hind legs are discussed. No data are at present available for *Stenocorixa*. The taxonomic position (isolation) of the two subfamilies is briefly discussed.

Diaprepocorinae Lundblad, 1928

Single extant genus *Diaprepocoris* Kirkaldy, 1897, type species *D. barycephala* Kirkaldy, 1897. Within the *Diaprepocorinae*, Popov (1971) in-

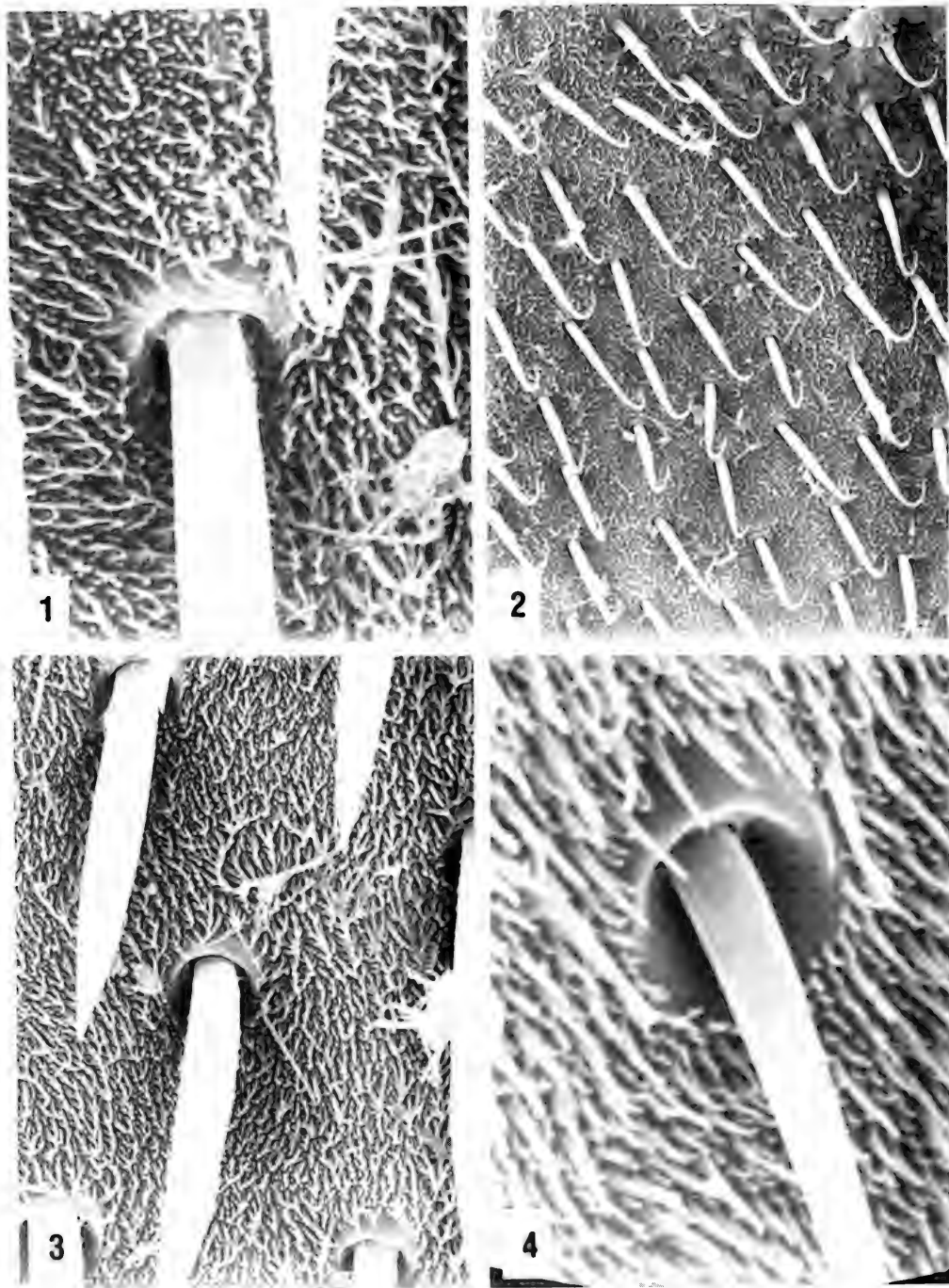
cludes *Gazimuria scutellata* Popov, from the lower Jurassic, Akutaev Series, Chitin Province, East Transbaikals and *Karataviella brachyptera* Becker-Migdisova from upper Jurassic, Chayan Region, Chimkent Province, South Kazakhstan. Walton (1940) split the *Diaprepocorinae* into two tribes using the structure of the female pala:

Diaprepocorini. – Female pala digitiform, few sieve hairs (about 10) and short. Type/Genus species *Diaprepocoris barycephala*.

Corixanectini. – Female pala short and broad, inner side flattened and fringed with numerous long sieve hairs. Type/Genus species *Corixanecta zealandiae* Hale.

Stenocorixinae Hungerford, 1948

Single extant genus, *Stenocorixa* Horvath, 1927, type species *S. protrusa* Horvath, 1927, monobasic. Jaczewski (1928) placed *Stenocorixa* in the *Corixinae*; Poisson & Jaczewski (1928) discussing the systematic position of *Stenocorixa* concluded that the poorly developed abdominal asymmetry, shape of the pala claw and other features suggested a relationship with *Cymatia* Flor. They ended by stating 'The generic distinctness of *Stenocorixa* Horv. is beyond any doubt and even as a separate genus it seems to stand rather apart of the other genera of the subfamily *Corixinae*'.



Figs. 1-4. *Diaprepocoris barycephala* Kirkaldy. - 1, corium, double hair pile, note collapsed microtrichia and longitudinal ridges on macrotrichia $\times 3200$; 2, inner lateral margin of clavus, note 'shephards crook' macrotrichia $\times 400$; 3, middle of corium $\times 800$; 4, membrane of elytra, note more erect microtrichia and enlarged socket of macrotrichia $\times 6400$. Reduction 84%.

DESCRIPTIVE PART

Diaprepocoris, structure trichia

Macrotrichia of the clavus and corium varying in shape. The hairs along the inner margin of the corium are apically curled over forming a 'shepherds crook' (fig. 2) and are longer and thinner than those on the inner areas adjacent to the clavus (fig. 3). The microtrichia are densely packed and resemble a plastron-like layer however, as they have collapsed and become matted, they clearly do not function as a plastron. The distribution of the microtrichia is fairly uniform over the clavus and corium. The membrane differs in that the microtrichia do not seem to have collapsed as much as those on the clavus and corium (fig. 1 clavus; fig. 4 membrane). The shape of the sockets within the microtrichia from which the macrotrichia arise, structurally suggests that the latter can be elevated and depressed (fig. 1). The macrotrichia are rather more slender and fewer in number on the membrane. Those on the elytra are longitudinally ridged (fig. 1). The division between the double hair layer and the edge of the forewing is distinct (fig. 5). The lateral margin at the nodal furrow shows a scale-like appearance with no hair layers (fig. 6).

Stenocorixa, structure trichia

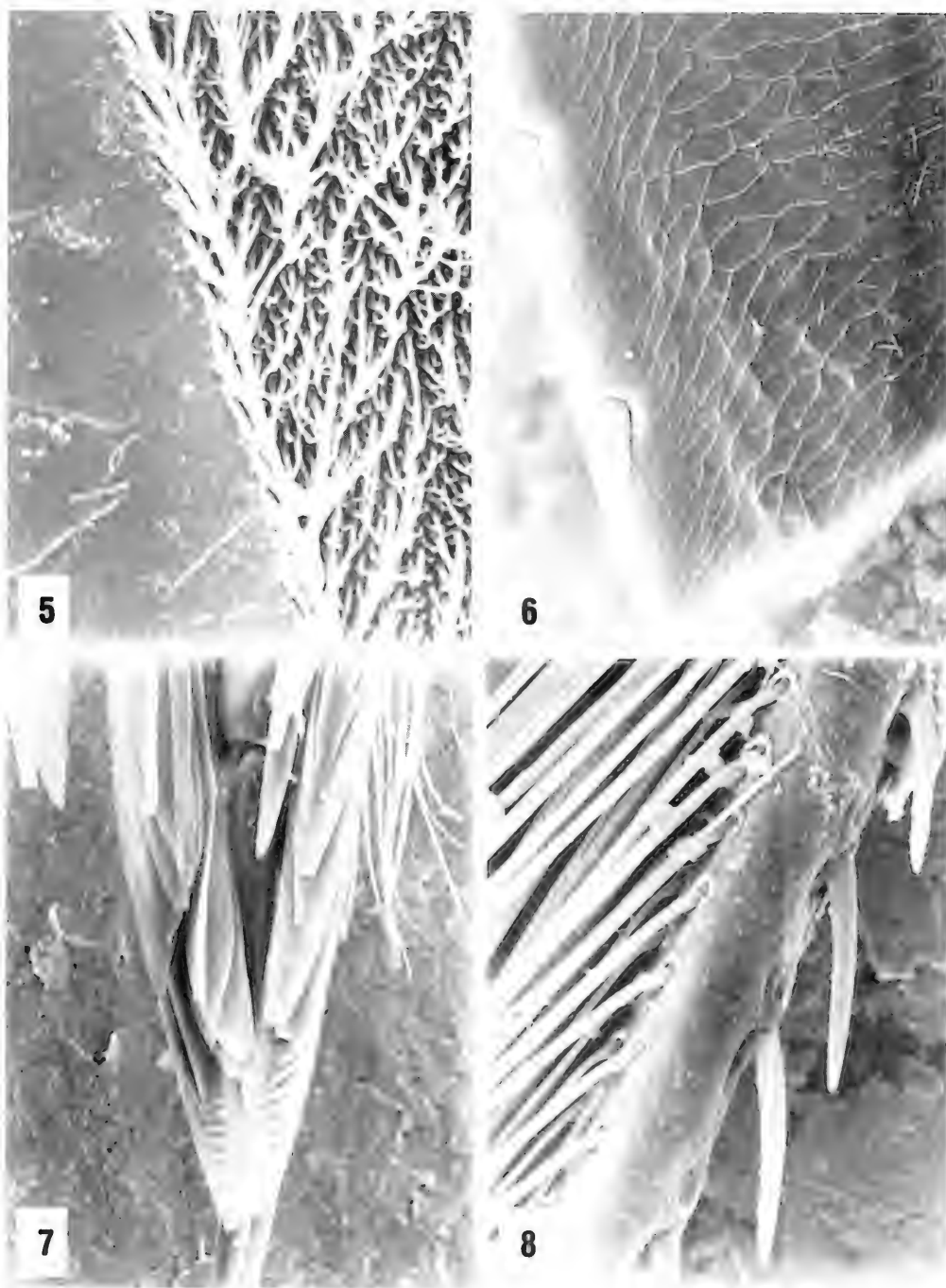
Unlike nearly all other genera of corixids, the pronotum and hemelytra are not rastrate, but smooth and shining with scattered long strap-like hairs arising from angled depressions, each with a complete basal ring (fig. 13). Caudad of each depression, an elongate channel within the clavus-corium, the strap-like hairs are almost certainly lodged in the channel(s) when the corixid is swimming.

Diaprepocoris, cuticular blades and swimming hairs

The hind tarsi of *Diaprepocoris* have in addition to the rows of swimming hairs, fringes of cuticular blades as long or longer than their respective tarsal segments. When not in use, they overlie each other like a venetian blind (fig. 7). Fanned out they increase the surface area of the tibiae-tarsi. The spread of the blades increases the surface area of the 1st tarsus along the leading edge by 3.5×10 (this and following figures approximate) – trailing edge has a greater density of fine swimming hairs overlying a row of blades increasing the surface area by 10×2 . The leading edge of 2nd tarsus has a row of blades decreasing in length distally, increasing surface area by 3.0×10 – trailing edge has

fewer swimming hairs, the blades are roughly all the same length, increasing surface area by 2.0×10 . The cuticular blades thus greatly increase the surface area (figs. 17, 18). According to Nachtigall (1974) cuticular blades create about 90% thrust of that of a solid object of equal size in the Gyrinidae (Coleoptera).

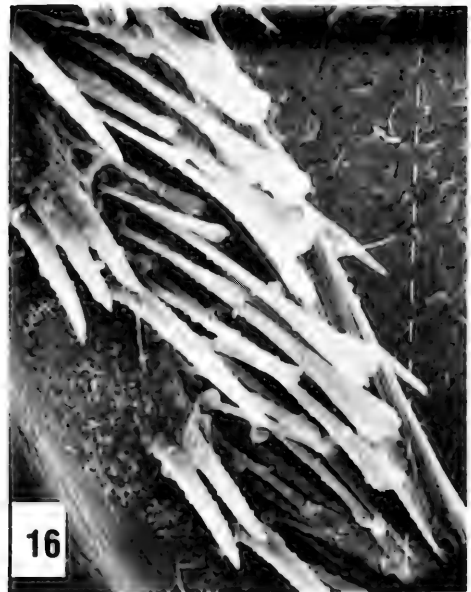
The blades of *Diaprepocoris* appear to have a function similar to those of gyrinids, the latter also use their middle legs when swimming. The hind coxae of *Diaprepocoris* conform to the usual corixid form. The ventral surface of the coxae is flattened to accommodate the trochanter-femur in the full recovery position, the femur forming a 33° angle with the midline of the body. The flattened area is partially enclosed by the tip of the metaxyphus and prevents excessive rotation of the hind leg (fig. 19). Schenke (1965, 1966) gives an account of a corixid swimming using *Corixa punctata* Illiger as a model. There are striking differences between the two genera. *Corixa* has a complex arrangement of rows of hairs, each with an incomplete basal ring, this enables the hairs to be folded flat against the leg during the recovery stroke. The tarsal hairs are supported by a row or rows of stout flexible spines which function in a similar fashion. There are few hind tarsal spines on *Diaprepocoris* compared with *Corixa*; *D. barycephala* 1st tarsus has between 10–13 spines in each of three lateral rows, one either side of the trailing edge and one along the leading edge. All the spines are semi-erect and probably rotate in much the same way as *Corixa*. The fringes of swimming hairs are arranged in a distinct manner. According to Schenke (1965) there are in excess of 5000 hairs on each rowing leg of *Corixa*. In *Diaprepocoris*, the leading edge of the 1st tarsus has about 30 long hairs, each having an incomplete basal ring (fig. 8) and a larger number along the trailing edge. Second tarsus with 8 long hairs along the leading edge and about 30 along the trailing edge. Figure 9 shows the incomplete basal rings of the cuticular blades in the recovery position, fig. 10 shows the folding of the blades on the 2nd tarsus partially overlapping the apical claws and extreme length of some of the blades. The hind tibiae moderately spinose (fig. 23) interspersed with hairs, some are expanded distally with a series of fine incisions (fig. 11). These modified hairs may reduce drag and loading on the hind legs, another function may be to move expired gas backwards over the elytra prior to the corixid surfacing to renew its gas store. The distribution of the explanate hind tibial hairs and cuticular blades of the tarsi are not uniform throughout the genus, *D. barycephala* (fig. 17), *D. personata* Hale (fig. 18) and *D. pedderensis* Knowles (figs. 20, 21). There is also variation in the development of the swimming



Figs. 5-8. *Diaprepocoris barycephala* Kirkaldy. – 5, outer lateral margins of corium and edge of double hair pile layer $\times 3200$; 6, lateral margin of forewing at nodal furrow with scale-like surface $\times 800$; 7, overlapping cuticular blades on hind tarsus $\times 200$; 8, hind tarsi, note incomplete basal rings $\times 400$. Reduction 84%.



Figs. 9-12. *Diaprepocoris barycephala* Kirkaldy. - 9, base of cuticular blades showing the incomplete basal rings $\times 800$; 10, cuticular blades on hind tarsi, note extreme length of blades $\times 50$; 11, incised hairs on the hind tibia $\times 800$; 12, immature *Diaprepocoris*, hind tarsus $\times 50$. Reduction 84%.



Figs. 13-16. *Stenocorixa protrusa* Horvath. – 13, elytra with single strap-like hair, note channel in elytra $\times 3200$; 14, explanate hind tarsi with cuticular blades $\times 24$; 15, explanate hind tarsi, note length and density of blades $\times 50$; 16, incised hairs on hind tarsi $\times 400$. Reduction 84%.

hairs on the middle legs; in *pedderensis* none are visible on a slide mounted leg (fig. 22), *personata* has about 20 hairs visible on the tibia and *barycephala* has about 50 hairs on the tibia and two rows of about 60 hairs on the tarsus.

Stenocorixa, cuticular blades and swimming hairs

The hind tarsi of *Stenocorixa* (fig. 14) are the most explanate of all the corixids, they most closely resemble those of *Lethocerus* (Belostomatidae, Heteroptera). The cuticular blades are extremely long forming a dense matted fringe (fig. 15). It has not been possible to determine from available preparations if each of the blades have an incomplete basal ring q.v. *Diaprepocoris* (fig. 9). The long swimming hairs fringing the rows of blades each appear to have incomplete basal rings. The trailing edge of the 1st tarsus has about 10 groups of stout semi-erect spines, between each group, a single thicker spine. The rows partially enclose several rows of long fan-shaped hairs which are deeply incised distally (fig. 16), it is likely that these hairs have a similar function to those of *Diaprepocoris*.

The fine structure of the clavus and corium of *Stenocorixa* does not suggest that it has a large supra-alar gas store, its overall streamlined appearance is totally different from that of *Diaprepocoris*. The complete basal rings would prevent the hairs laying flat against the forewings and would presumably cause minor eddies over the dorsum of the swimming corixid. The hairs are too few in number to act as a hydrofuge layer and may have some sensory function or be used for manoeuvring nektonically.

There is a rather greater degree of flexibility between the hind tibiae-tarsi than in *Diaprepocoris*. The hind tibiae of *Stenocorixa* have a pair of prominent projections distally. The acuminate insertion of the tarsus within the tibia suggests that there is considerable flexibility which would increase the corixids manoeuvrability. The 2nd tarsus is capable of partial folding as in the Gyrinidae, this would be advantageous in the recovery stroke reducing drag. The hind legs of *Stenocorixa* are pro-rata much longer than those of *Diaprepocoris*.

Diaprepocoris: hind tibiae not explanate and not reaching the end of the abdomen.

Stenocorixa: hind femur-tibia-tarsus explanate, tibia reaching the end of the abdomen.

The power stroke of *Stenocorixa* may exert a greater propulsive effort, the folding hind tarsi reducing drag during the recovery stroke. The relative shortness of the hind legs of *Diaprepocoris* with possible reduction of energy in the power

stroke may be compensated for by the supra-alar gas store, this would enable the corixid to stay submerged for longer periods, thus avoiding predators. The extra buoyancy would however, also mean that the corixid would need to keep up a high level of power strokes to maintain depth and attitude when submerged and not resting on submerged objects.

DISCUSSION

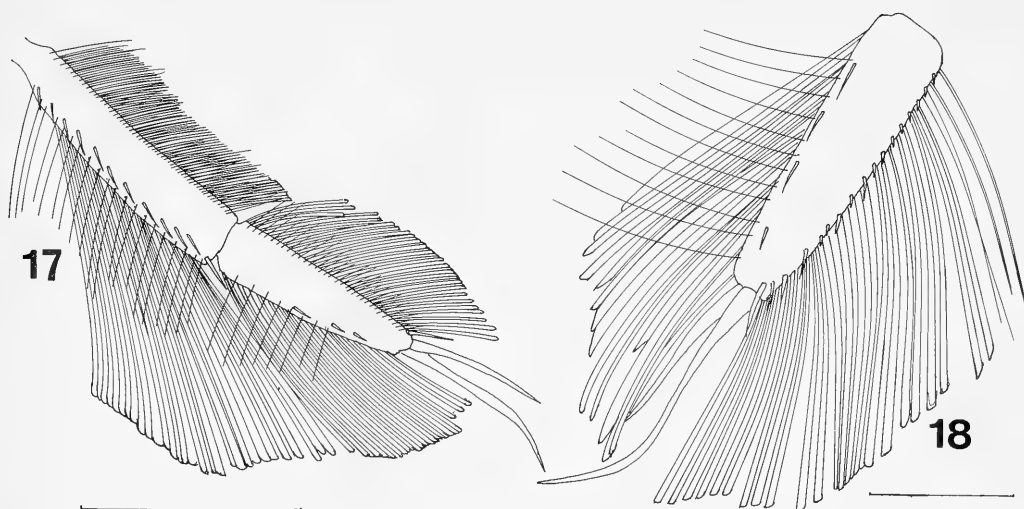
Thorpe & Crisp (1949) group aquatic animals with hydrofuge hairs in four categories, placing *Corixa* (Corixinae) in group III, members of which must surface at intervals to renew their gas stores. They are bouyant rather than heavier than water and often have a double hair pile.

Diaprepocoris according to Parsons (1976) has a much larger exposed dorsal air store covering the scutellum and forewing; the Micronectinae Jaczewski have the supra-alar store restricted to the anterior part of the embolium and the anterior-most part of the claval suture; the Corixinae Jaczewski have a slightly larger air store extending the length of the embolium, anterior part of the clavus suture and that part of the clavus covered by the pronotum. The mesonotal air store of the Micronectinae and Corixinae covered by the pronotum. As a form of air bubble respiration, *Diaprepocoris* has a much larger gas store than most other corixids, in addition to the supra-alar store, it has sub-alar gas stores beneath the forewings and over much of the venter.

The presence of large supra-alar air stores and sub-alar stores may increase the buoyancy of *Diaprepocoris*, the buoyancy levels possibly being related to the density of swimming hairs and cuticular blades on the hind legs. Possible secondary functions of the external gas layer may be either as a flexible skin which would enable the corixid to swim with less friction. With the exception of *D. pedderensis*, all *Diaprepocoris* species are relatively short and squat, their greatest width being just over half total length. An alternative function may be acoustic; Theiss (1982) has shown that in *Corixa*, the cervical air store i.e. air stores formed by the posterior and lateral parts of the head being flattened forming flanges which overlap the prothorax, are used in the generation and radiation of sound, thus the dual function of air stores has been demonstrated.

Taxonomy

Diaprepocoris and *Stenocorixa* are the most distinctive genera of the extant Corixidae. Characters common to both subfamilies are:



Figs. 17-18. *Diaprepocoris* hind tarsi. – 17, *D. barycephala* Kirkaldy, scale line 1 mm; 18, *D. personata* Hale, scale line 0.25 mm.

- Hind tarsi fringed with cuticular blades
- Little difference between the male and female palae

The *Diaprepocorinae* share a set of characters which distinguishes the subfamily from all others:

1. Ocelli on vertex between compound eyes (fig. 24)
2. Fore tibia-tarsus fused (fig. 25)
3. Tarsal claws of hind legs apical (figs. 17, 18 and 21)
4. Muscle attachment to male genital capsule dorsal
5. Female ovipositor with a recognisable blade-like structure

The *Stenocorixinae* share a limited set of characters which distinguish the subfamily:

1. Clavus and corium smooth without microtrichia (fig. 13)
2. Clavus and corium with scattered long strap-like hairs
3. Abdominal asymmetry of male 6-7th tergites hardly differing from female
4. Male left paramere absent

Various proposals have been made regarding the validity of the corixid subfamilies. Leston (1955) partially summarised the proposals of China (1943) and Hungerford (1948) and observed that most authors treat the Corixidae as a monophyletic group. Popov (1971) altered this concept to include the *Shurabellidae* (*Shurabella lepyronopsis* Becker-Migdisova, Liassic fossil). The Corixoidea should be considered a holophyletic group sensu Ashlock (1971).

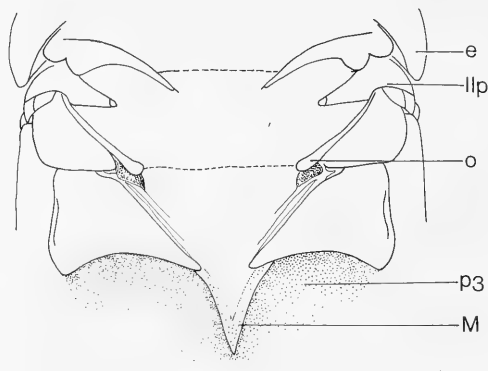
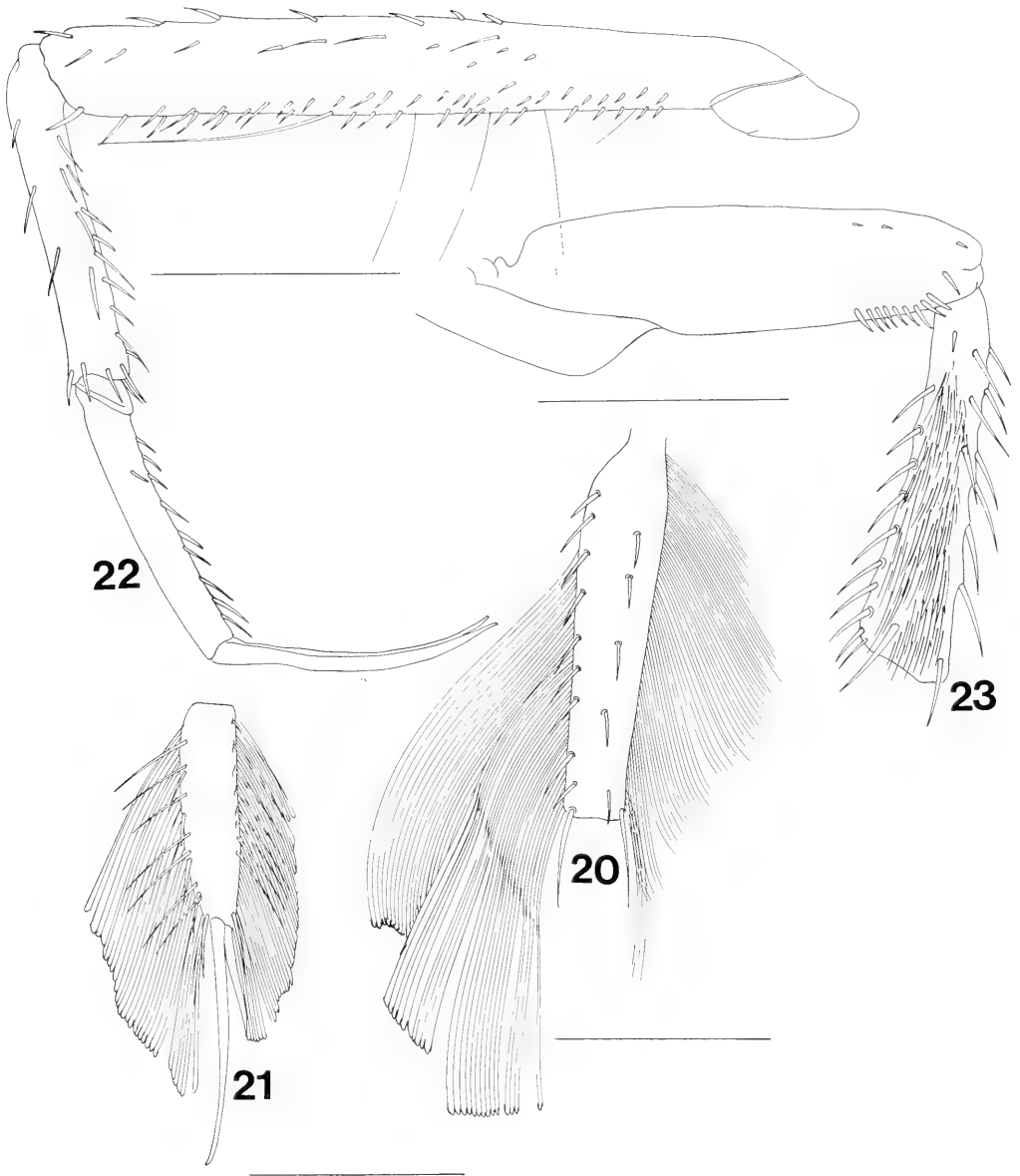


Fig. 19. *Diaprepocoris personata* Hale: metaxyphus and ancillary structures. Abbreviations; e, eye; 11p, lateral lobe of prothorax; o, osteole of scent gland; P3, insertion of 3rd coxa; M, metaxyphus, scale line 1 mm.

Hungerford (1948) split the Corixidae into six subfamilies:

1. Groups with large exposed scutellum
..... *Diaprepocorinae* and *Micronectinae*
- Groups with scutellum hidden 2
2. Hemilytral groove absent *Stenocorixinae*
- Hemilytral groove present 3
3. Rostrum without transverse sulcations or nodal furrow, *Cymatiinae*
- Rostrum with transverse sulcations and nodal furrow *Corixinae* and *Heterocorixinae*



Figs. 20-23. *Diaprepocoris pedderensis* Knowles. – 20, 21, hind tarsi, scale line 1 mm; 22, middle leg, scale line 0.5 mm; 23, hind femur and tibia, scale line 0.5 mm.

Popov (1986) recognised three extant subfamilies viz. Corixinae, Diaprepocorinae and Micronectinae. Popov (1971) speculating on the affinities of *Stenocorixa* noted that the male genital capsule differed from all other corixids and that further study of the aberrant groups (*Stenocorixa* and *Heterocorixa* etc.) would be necessary before the status of these groups was fully understood.

Nachtigall (1974) comments 'The rowing legs of recent water dwellers are considerably more flattened than those of fossil water dwellers or the legs of terrestrial relatives'. Within the Corixidae, both extant and fossil, there is little apparent distinction. The fossil genus *Gazimuria* looks like a form of *Diaprepocoris*, *Stenocorixa* has explanate hind legs, *Corixa* moderately so, but there does not seem to be a steady progression throughout the corixid genera. As no corixids are remotely terrestrial, Nachtigall's observations do not seem to be applicable.

Immature stages

Diaprepocoris barycephala 4th-5th instar: The front leg (fig. 25) closely resembles the adult. As in all immature corixids the front tibia-tarsus are fused, this character persists in the adult *Diaprepocoris*. The middle leg also closely resembles the adult form, but lacks the swimming hairs on the tibia-tarsus (fig. 26). The hind leg similar to the adult with prominent cuticular blades (figs. 12 & 27). The hind tarsus is one-segmented as in all known immature corixids.

Immature stages of *Stenocorixa* were not available for study.

ACKNOWLEDGEMENTS

The Leverhulme Foundation, London; CSIRO Division of Entomology, Canberra and the Australian Biological Resource Study, Canberra are thanked for grants in aid towards a field-trip in 1979. Dr. W. D. Williams, Adelaide University, Dr. I. A. E. Bayly and Dr. P. S. Lake, Monash University sent me *Diaprepocoris* specimens. The SEM figures were made by Mrs Barbara Luke, Zoology Department, Oxford University, courtesy of Professor D. S. Smith (Hope Professor).

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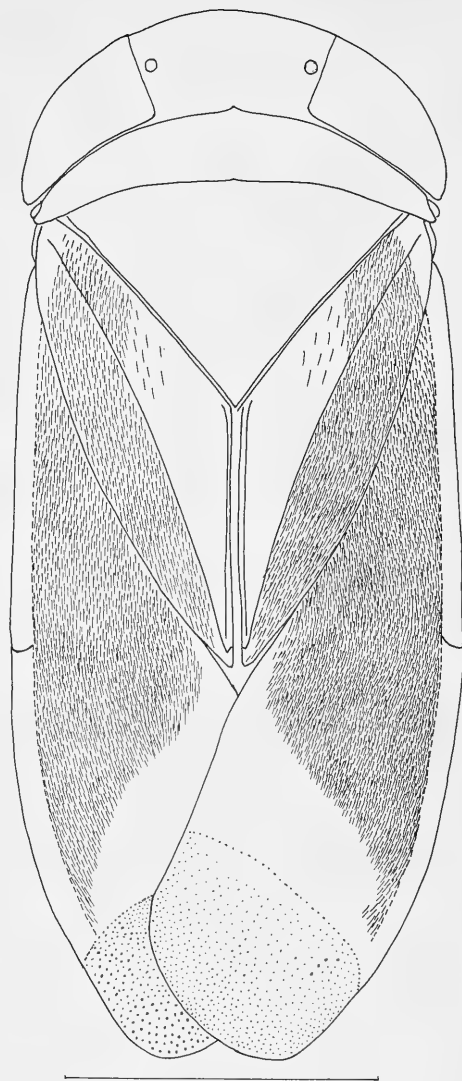
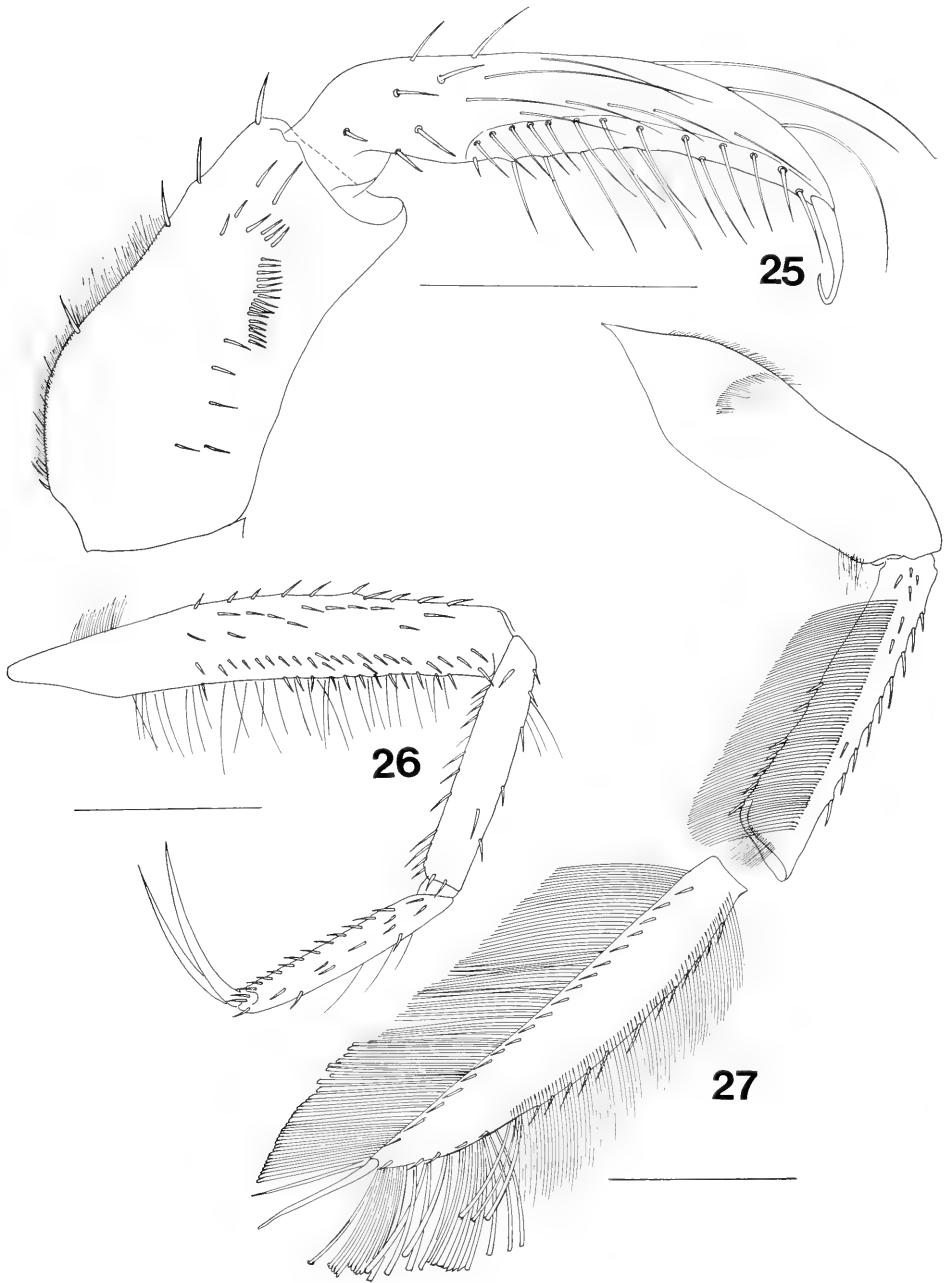


Fig. 24. *Diaprepocoris pedderensis* Knowles, male dorsal habitus, scale line 1 mm.

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Figs. 25-27. *Diaprepocoris barycephala* Kirkaldy, immature. – 25, front leg, scale line 0.5 mm; 26, middle leg; 27, hind leg, scale line 0.5 mm.

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NAUCORIDAE, NEPIDAE AND NOTONECTIDAE, MAINLY FROM SULAWESI AND PULAU BUTON (INDONESIA)

Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), I.

Nieser, N. & P. Chen, 1991. Naucoridae, Nepidae and Notonectidae, mainly from Sulawesi and Pulau Buton (Indonesia). Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), I. – Tijdschrift voor Entomologie 134: 47-67, figs. 1-21. [ISSN 0040-7496]. Published 1 July 1991.

Apart from new records for many species, mainly for Sulawesi, P. Buton and Sabah (N. Borneo), eight new species are described. Naucoridae: *Aphelocheirus breviculus* sp. n. (Sabah), *A. robustus* sp. n. (Sulawesi), *Coptocatus stereos* sp. n. (Sabah); Nepidae: *Ranatra sulawesii* sp. n. (Sulawesi); Notonectidae: *Enithares caesaries* sp. n., *E. lansburyi* sp. n., *E. phenakismos* sp. n. (all from Sulawesi) and *E. skutalis* sp. n. (P. Buton).

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Key words. – Sulawesi; Buton; Sabah; Nepomorpha; keys; new species.

During the last decades the study of Nepomorpha and Gerromorpha of Indonesia and Malaysia is making some progress (see e.g. Lansbury 1964-1985, La Rivers 1970, Polhemus 1986, Polhemus & Polhemus 1988). New expeditions to formerly unexplored areas and even rather occasional trips to already explored regions (see e.g. Nieser & Chen 1991), however, are still adding new species and new distributional data to our knowledge. As in many other groups, a high proportion of the species in this region seems to have limited ranges. In water bugs these restricted ranges are usually apparent in stream inhabiting species, whereas many of the widespread species occur in or on ponds in cultivated areas.

The species dealt with in this paper were mainly collected by J. P. Duffels, J. van Tol and N. Nieser on several expeditions to the eastern part of Sulawesi, the nearby island of Buton and Borneo.

Keys to the Malesian genera are included. Keys to species of Sulawesi and Pulau Buton are given for most genera, but they should be used with extreme caution as the fauna of the region is still poorly known.

Measurements are in millimeters and present the range or the (arithmetic) mean based on five randomly chosen specimens, or in case there are less than five, on all specimens available. The width of the head is measured across the eyes.

MATERIAL

A list of collecting localities of N. Nieser is presented in appendix 1. Sampling stations of J. P. Duffels and J. van Tol are partly connected with 'Project Wallace' and with the '1989 RMNH Expedition to Sulawesi'. Data on the latter expedition will extensively be described in a separate paper (Van Tol et al. in prep.). All other sampling stations of both collectors, including those on Borneo, are summarized in appendix 2.

In addition to these recent collections, miscellaneous Malesian material in the RMNH collection has been included. Specimens collected by J. P. Duffels are deposited in ZMA, those by J. van Tol in RMNH, and those by N. Nieser in his own collection, unless stated otherwise. Deposition of material is specified only with rare or new species.

The areas in Sulawesi used with the localities agree with the Indonesian provinces, viz. Sulawesi Utara for Northern Sulawesi (Celebes), Sulawesi Tengah for Central Sulawesi and Sulawesi Tenggara for Southeastern Sulawesi. Pulau Buton is mentioned separately although it belongs administratively to Sulawesi Tenggara (see Whitten et al. 1988). Localities are in Indonesia, unless stated otherwise.

Collections from which material has been studied (with abbreviations in brackets): Museum

Zoologi Bogor, Bogor, Jawa (MBBJ); Bagian Pertanian, Universitas Haluoleo, Kendari, Sulawesi (BPUH); J. T. Polhemus collection (University of Colorado Museum), Englewood, Co., U. S. A. (JTPC); Snow Entomological Museum, University of Kansas, Lawrence, Kansas, U. S. A. (SEMC); N. Nieser collection, Tiel, The Netherlands (NC); Oxford University Museum, Oxford, United Kingdom (OXUM); National Museum of Natural History (Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH); Zoologisch Museum, Afdeling Entomologie, Amsterdam, The Netherlands (ZMA).

ACKNOWLEDGEMENTS

Thanks are due to Dr J. P. Duffels (ZMA) and Mr. J. van Tol (RMNH) for putting specimens in their care to our disposal; to Dr I. Lansbury (OXUM) for discussing some Notonectidae and to Dr I. Made Ebeneser (BPUH) for showing the senior author some interesting localities.

SYSTEMATIC PART

NAUCORIDAE

Key to Indonesian and East Malaysian genera

1. Rostrum slender, longer than fore femora, reaching to middle coxae (Aphelocheirinae) *Aphelocheirus* Westwood
- Rostrum stout, very broad at base, much shorter than fore femora (Naucorinae) 2
2. Rostrum inserted at anterior margin of head, labrum distinct and well developed 3
- Rostrum inserted in a deep excavation, distinctly posterior to the apical margin of head, labrum often greatly reduced (Cheirochelini) 5
3. Fore tarsi one-segmented, with one single very small claw (Naucorini) *Naucoris* Fabricius
- Fore tarsi two-segmented, with two claws, which are often very inconspicuous (Laccocorini) 4
4. Labrum more or less equilaterally triangular with an acute tip *Laccocoris* Stål
- Labrum with sides shorter than base and tip broadly rounded *Heleocoris* Stål
5. Head ventrally with well developed grooves in which fit the antennae *Coptocatus* Montandon
- Antennal grooves absent 6
6. Ventral margin of prothorax with a conspicuous pit covered with a membrane or specialized pilosity (static sense organ), body elongate,

- connexival angles blunt, not spinose, consequently lateral edge of abdomen more or less continuous 7
- Static sense organ on ventral margin of prothorax absent, body oval, connexival angles sharp, usually spinose, consequently lateral edge of abdomen distinctly serrate 9
 - 7. Static sense organ slightly anterior to midway of lateral margin of prothorax, ventral keel of head strongly developed with an anterior spine-like tip, which is at least as long as first rostral segment *Idiocarus* Montandon
 - Static sense organ near or at antero-lateral angle of prothorax, ventral keel of head normal, without a prominent anterior spine 8
 - 8. Static sense organ rounded, placed at extreme antero-lateral angle of prothorax, which is cup-shaped; anteclypeus short, broadly and evenly rounded *Nesocricus* La Rivers
 - Static sense organ elongate, placed half to three-quarters of its length caudad to antero-lateral angles of prothorax; anteclypeus quite long with sinuate margins producing a medio-anterior lobe *Tanyricrus* La Rivers
 - 9. Mesotibia distally with five or six decreasingly sized, transverse rows of dense, short spines *Cavocoris* La Rivers
 - Mesotibia with at most two of such rows of spines 10
 - 10. Anteclypeus prolonged, overhanging part being half to three-quarters the length of labral base *Warisia* La Rivers
 - Anteclypeus short, overhang at most one third of the length of labral base 11
 - 11. Abdominal venter showing only four segments *Quadricoris* La Rivers
 - Abdominal venter showing the usual five segments 12
 - 12. Larger species, length over 7 mm; abdomen asymmetrical *Sagocoris* Montandon
 - Smaller species, length slightly less than 7 mm; abdomen symmetrical *Aptinocoris* Montandon

Remarks. - Except for *Sagocoris*, which has also one representative in the Philippines, the last mentioned eight genera are restricted to New Guinea.

In the species of Naucoridae described below, the first abdominal segment is not visible. The numbers used are the morphological homologous numbers, thus 'tergites 2-8' are visible as tergites 1-7.

Aphelocheirus Westwood, 1833

Southeast Asiatic species of the genus were re-

cently revised by Polhemus & Polhemus (1988). About 18 species are known from Malesia, including the Philippines, but more species are to be discovered. Species of *Aphelocheirus* are easily overlooked by the casual collector as most burrow in the bottom of streams. Thanks to their plastron respiration they do not need to surface to refill their air store.

Key to *Aphelocheirus* of Sulawesi

1. Lateroposterior spines of connexiva 4-5 short and broad; body length of male 8.9-9.1 mm, of female 8.5-8.8 mm (Sulawesi Selatan)
..... *A. celebensis* Polh. & Polh.
- Lateroposterior spines of connexiva 4-5 rather long and acute; body length of male c. 10 mm, of female more than 9.2 mm 2
2. Male: Left paramere with a broad hooked apex (fig. 5). Female: Genital operculum short and broad with convex caudo-lateral angles (fig. 3) (Sulawesi Tenggara) *A. robustus* sp. n.
- Male: Left paramere with a slender curved apical part. Female: Genital operculum rather long and slender with apical lateral margins very slightly concave (Sulawesi Tengah)
..... *A. lorelindu* Polh. & Polh.

Aphelocheirus lorelindu Polhemus & Polhemus

Aphelocheirus lorelindu Polhemus & Polhemus, 1988: 190-192, figs. 18-21, 164.

Material. - Sulawesi Tengah: Palu, 50 km SE of: Lore Lindu NP, Sopa river near Dongi Dongi, 950 m, SJ 86, 8 Dec 1985, J. van Tol, 3 ♀, (RMNH).

Distribution. - Known only from the Lore Lindu N. P. in Central Sulawesi, and surrounding areas.

Aphelocheirus breviculus sp. n. (figs. 1-2)

Type material. - Holotype ♀: Malaysia: S. Sabah: 105 km S of Beaufort, Long Pasia area, Sungai Ritan, 4°24'N 115°42'E, 1160 m, undisturbed evergreen tropical rainforest, 9.IV.1987, J. van Tol & J. Huisman (RMNH). - Paratypes: 2 ♀ with same data (RMNH, NC).

Description

Brachypterous female. - Rather small species, form elongate oval, length 7.7-8.1 mm, width of head 1.8-1.9 mm, maximum width across abdomen 4.9-5.1 mm.

Colour greyish brown, head on dorsal side yellow to light brown, posteriorly darker, with black eyes; pronotum, hemielytra and tergites greyish to brown, margins and scutellum paler; legs and ven-

ter yellowish to light brown, central part of thoracic and abdominal sternites greyish, pruinose, with sparse golden pubescence.

Head. Shining, coarsely punctate, produced ahead of eyes for distance equal to 0.5 the length of an eye; eyes twice as long as wide, outer margins sinuate, due to weakly developed antero-lateral flange; anterior / posterior interoculus = 1.3/1.0 mm.

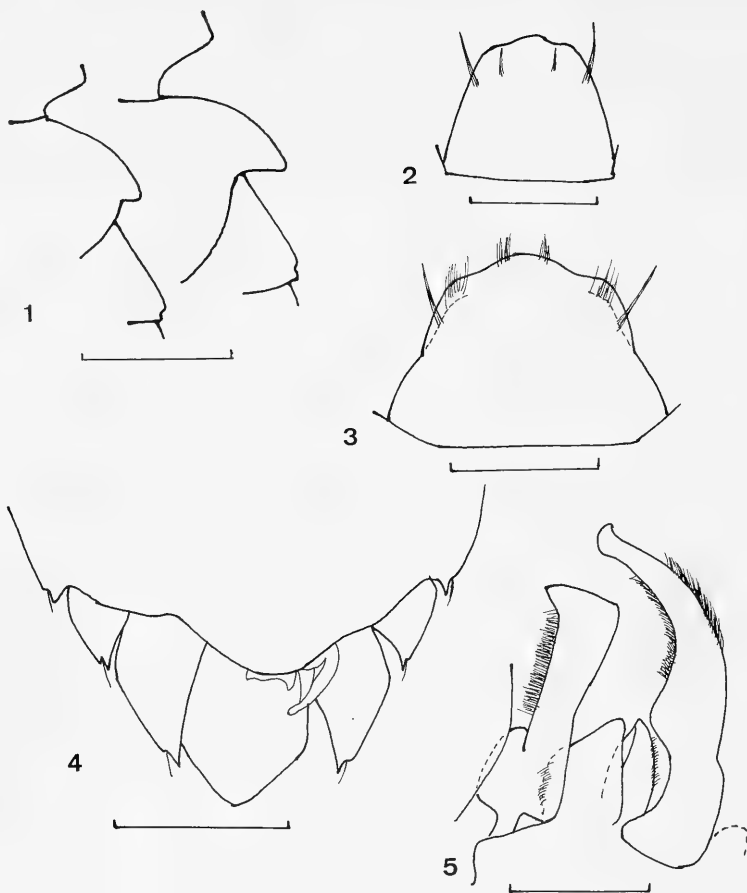
Thorax. Pronotum shining, roughly punctate, antero-medially rugose; very sparsely set with inconspicuous short fine pale setae, width / length 3.5; lateral margins bearing about twelve stout minute erect setae. Scutellum shining, rugose, width / length 2.5, lateral margin hardly sinuate, shallow transverse sulcus present along anterior margin (to fit the posterior margin of pronotum). Hemielytra not touching medially, leaving an area 0.4 mm wide of metanotum uncovered; posteriorly not reaching the hind margin of abdominal tergite 2, surface punctate-rugose, claval area shining, dull in remainder, clavus not delineated; embolar margin evenly curving anteriorly, its posterior angle strongly produced laterally (fig. 1).

Abdomen. Dull, rugose with narrow shining margins which bear 5-7 minute erect setae in small indentations, posterior indentation of each segment bearing two or three of these minute setae and a few longer, easily detachable, setae. Tergites 2-8 exposed, bearing very few short thin pale recumbent setae, paired glandular openings present, but indistinct on posterior margin of tergite 3. Posterolateral angles of tergites 3-7 bluntly and broadly spinose, more distinctly produced posteriorly.

Ventral side. Length of antennal segments 1-4 is 0.09, 0.23, 0.23 and 0.42 mm. Labrum shining, anterior margin evenly rounded, rostrum shining, length 3.2-3.4 mm, reaching middle trochanters. Prosternum with weak median carina, propleura with inner projections notched; mesosternum pruinose with a median carina, tumescent posteromedially; metasternum pruinose, metaxiphus small, apically pointed. Abdomen pruinose, sternites 3 and 4 bearing rounded projections medially on posterior margins, posterior margins of sternites 4 and 5 lacking rearwardly directed stout setae medially; genital operculum with posterolateral angles developed, resulting in a sinuate posterior margin; narrow tufts of long setae at lateral margins and intermedially in apical third (fig. 2).

Legs. Set with fine gold setae, fore femur, tibia and tarsi with thick hair pads on inner surface. Fore, middle and hind coxae with combs of long light brown setae on interior margins. Middle leg, trochanter, femur, tibia and tarsi with thick yellow hair pads on ventral faces; femur sparsely set with

Figs. 1-5. *Aphelocheirus* species. – 1, Apex of embolium of *A. minor* (left) and *A. breviculus* (right); 2, Genital operculum of ♀ *A. breviculus*; 3, idem, *A. robustus*; 4, *A. robustus*, apex of abdomen of brachypterous ♂, dorsal view; 5, *A. robustus*, parameres, ventral view. Scales: 1 mm (1-3), 2 mm (4), 0.5 mm (5).



short stout reddish spines, bearing 6-8 long erect setae on posterior margin; tibia rather densely set with short stout reddish spines, bearing about four long setae on anterior margin and one row of red spines apically. Hind leg, femur and tibia sparsely set with short stout reddish spines, tibia also with an apical transverse row of reddish spines, tibia and tarsi bearing long swimming hairs on ventral surface. Claws of all tarsi shining, curved, with darker, reddish brown apices.

Comparative notes

This species runs to *A. labu* Polhemus & Polhemus and *A. minor* Polhemus & Polhemus in the key of Polhemus & Polhemus (1988). It shares with *A. minor*, which is also from Sabah, abdominal segments 3 and 4 bearing rounded projections medially on the posterior margins. *A. breviculus*, however, is one millimeter longer on average, has the angle of the embolium more produced (fig. 1), and

the ratio width / length of the pronotum greater than in *A. minor*, viz. 3.6 and 3.2 respectively. The eyes of *A. minor* are narrower, about three times as long as wide, while *A. breviculus* has its eyes twice as long as wide.

Etymology

Breviculus, a Latin adjective, meaning rather short, refers to the small size of the species.

Aphelocheirus robustus sp. n. (figs. 3-5)

Type material. – Holotype ♂ (brachypterous): Sulawesi Tenggara, K. Kolaka. Sungai Mowewe, 28. II. 1989, leg. N. Nieser, N8922 (RMNH). – Paratypes: 9 ♂ 14 ♀ (incl. 1 labelled allotype) brachypterous, 16 ♂ 7 ♀ macropterous, same data as holotype, deposited as follows 3 ♂ 3 ♀ brach., 3 ♂ 3 ♀ macr. (NC); 1 ♀ brach., 1 ♂ macr. (MBB); 1 ♂ 2 ♀ brach., 2 ♂ 1 ♀ macr. (JTPC); 1 ♀ brach.,

2 ♂ macr. (SEMC); 1 ♂ macr., 1 ♀ brach. (OXUM); 1 ♀ brach., 1 ♂ 1 ♀ macr. (RMNH); 1 ♂ 1 ♀ brach., 1 ♂ 1 ♀ macr. (ZMA).

Additional material. – 18 larvae IV/V, with same data as holotype.

Description

Brachypterous male. – Large species for this genus, form elongate oval, length 9.8–10.5 mm; width of head 2.2–2.3 mm; maximum width (across abdomen) 5.9–6.2 mm.

Colour. Somewhat variable. Dorsal side: head yellow with black eyes, pronotum yellow with anterior and posterior transverse dull brown band, scutellum yellow (most specimens) to brown, hemielytra brown with variable part posteriorly yellow, abdominal tergites dull brown with yellow posterolateral angles, genital segments yellow. Ventral side: head, including antennae yellow, rostrum pale brown, sternites brown with yellow lateral margins, legs and genital segments yellow.

Head. Shining, finely rugose, produced ahead of eyes for distance equal to $0.4 \times$ the length of an eye; eyes length / width = 2.4–2.5, outer margin sinuate due to weakly developed anterolateral flange; anterior / posterior interoculus = 1.35–1.40.

Thorax. Pronotum rugose, sparsely set with short fine pale setae laterally, apparently glabrous medially, width / length = 3.7–4.0; lateral margins bearing c. 10 stout minute erect setae. Scutellum rugose, appearing glabrous, width / length = 2.3–2.5, lateral margin hardly sinuate, shallow transverse sulcus present along anterior margin (to fit the posterior margin of pronotum). Hemielytra touching medially, reaching posteriorly to or just beyond base of abdominal tergite 3, surface rugose, set with sparse fine pale setae, embolar margin evenly curving anteriorly, bluntly terminated posteriorly in most specimens.

Abdomen. Weakly rugose, set with fine pale setae, tergites 2–8 exposed, paired glandular openings present medially on posterior margin of tergite 3, posterior margin of tergite 5 asymmetrical, with a medioposterior hump-like projection, which is delimited more clearly on the left than on the right (fig. 4), lateral margin of all segments with short stout setae, posterolateral angles of all tergites 3–7 spinose, with a few long pale setae at base of spinose angles.

Ventral surface. Length of antennal segments 1 to 4: 0.10, 0.20, 0.35 and 0.45 mm; rostrum glabrous, length 3.2–3.4 mm, reaching to middle coxae. Labrum yellow, shining, anterior margin evenly rounded. Prosternum with weak median carina, propleura with inner projections notched; mesosternum pruinose with a median carina, tumescent posteromedially; metasternum pruinose,

metaxiphus small and narrowly pointed. Abdomen pruinose, posterior margins of sternites 4 and 5 with six rearwardly directed stout setae medially; genital segments glabrous, shining.

Legs. Set with fine golden setae, fore femur, tibia and tarsi with thick hair pads on inner surface, claws well developed and curved in most specimens but in several short, stunted and not curved. Fore, middle and hind coxae with combs of long light brown setae on anterior margins. Middle legs, trochanter, femur, tibia and tarsi with thick yellow hair pads on ventral faces; femur sparsely set with short stout reddish spines bearing 6–8 long erect setae on posterior margin; tibia sparsely set with short stout reddish spines, bearing three long setae basally on anterior margin and one row of red spines apically. Hind leg, femur sparsely set with short stout reddish spines, tibia with reddish spines along interior margin, tibia and tarsi bearing long silvery swimming hairs on ventral surface, claws shining, curved. In several specimens middle and hind claws and sometimes tarsi stunted.

Male genitalia. Right paramere longest with long golden pubescence on right margin, apex rounded, left paramere hooked with thick golden pilosity on left margin. (fig. 5).

Brachypterous female. – Length 9.5–10.1 mm; width of head 2.2–2.3 mm; maximum width 5.8–6.0 mm. Subgenital plate triangular with narrow lateral earlike structure (fig. 3), longer lateral setae and shorter posterior setae spread out, not in narrow tufts.

Macropterous form. – As brachypterous, except length ♂ 10.6–11.0 mm, ♀ 10.0–10.6 mm. Pronotum well developed, subequal to maximum width of abdomen; scutellum larger and somewhat inflated; mesosternum inflated with broad rounded carina medially; hemielytra well developed (membrane broken off in some females), blackish in most fully mature specimens, leaving lateral part of connexiva uncovered; embolium with a blunt but distinct angle midway.

Comparative notes

This species runs to *A. lorelindu* Polhemus & Polhemus in the key to brachypterous specimens of Polhemus & Polhemus (1988); both species are very similar in general shape and size. The female subgenital plate of *A. robustus* differs from larger Southeast Asiatic *Aphelocheirus* by its small lateral 'ears'. The right paramere is narrower at base than *A. lorelindu* and *A. celebensis* Polhemus & Polhemus, its closest relatives. See also the key to the Sulawesi species.

Coptocatus stereos sp. n.

(figs. 6-7)

Type material. – Holotype ♂ (brachypterous): Malaysia: S. Sabah. 105 km S of Beaufort: Long Pasia area, Sg. Maga near confluence Sg. Pasia. 4°26'N 115°40'E, 1210 m asl., larger fast running stream in untouched lower montane evergreen rain forest, large boulders, rapids. 3 Apr. 1987. Leg. J. van Tol (RMNH).

Additional material. – 3 larvae instar V and 1 instar III / IV, same data as holotype (RMNH).

Description

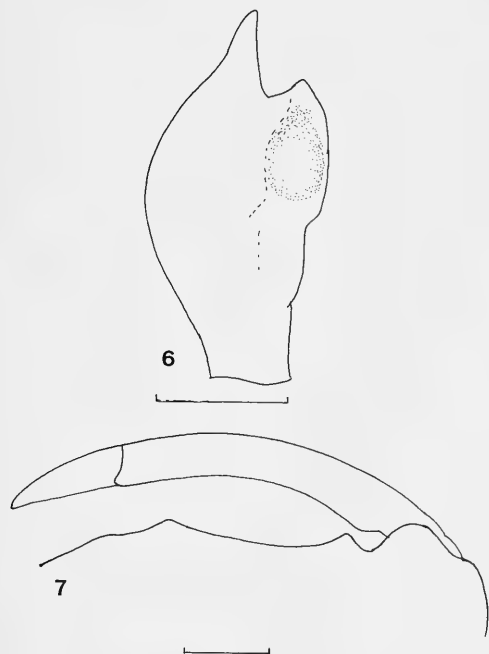
Holotype ♂. – Large, robust, highly streamlined and dorsoventrally flattened; general colour medium brown with yellowish spots. Length 20.4 mm, width of head 5.4 mm; width of pronotum 10.6 mm, maximal width 12.2 mm.

Head. Width / length 5.4 / 4.2 mm. Anteclypeus greatly produced, apex evenly rounded, projecting beyond rostrum for a distance greater than exposed rostral length when viewed laterally; eyes blackish, convex, roughly rectangular, length / width 1.8 / 1.2 mm, raised above level of vertex and separated from it by wide shallow sulci, lateral margins bearing a weakly developed flange; anterior / posterior interoculus 3.2 / 3.2 mm; vertex greatly produced posteriorly, extending rearwardly about one half the length of an eye; anteriorly with a pair of broad shallow sublateral depressions, tapering posteriorly.

Thorax. Pronotum width / median length 10.4 / 3.0 mm; lateral margins with narrow, raised darker and slightly crenulate ridge, posterolateral angles strongly produced, rounded. Scutellum width / length 5.0 / 2.8 mm, anterior margin strongly reflexed downward. Hemelytra brachypterous, extending to posterior margin of abdominal tergite 3 only, tips broadly rounded, surface set with fine yellowish granular microstructure (also present on other parts of body, although far less dense and less distinct), embolium anteriorly defined by a broad carina, explanate, lateral margin irregularly and shallowly crenulate, set with long recumbent light brown setae; hemelytral commissure with a small projecting tooth on left hemelytron distally, fitting into corresponding indentation of right hemelytron.

Abdomen. Medio- and latero-caudal parts of tergite 3 and all of tergites 4-8 exposed. Lateral margins with narrow ridges and a dense row of long light brown setae lying flat on tergites. Medially some patches of shorter setae at base of tergites, especially the lobes of tergite 8. Lateroposterior angles indented with blunt projections and a tuft of hairs in the indentation.

Ventral surface. Sternites pruinose. Gula and part of prosternum anterior to fore coxae with a



Figs. 6-7. *Coptocatus stereos*. – 6, Left paramere n. Scale 0.5 mm; 7, Tibiotarsus and anterior margin of femur of fore leg. Scale 1 mm.

Etymology

Robustus, a Latin adjective, refers to the large size of the species within the genus.

Remarks

The type locality is a lowland stream, 2.5 to 10 m wide, flowing through woodland with fields and small settlements close by. *Aphelocheirus* was found at shallow, partly shaded places, with moderate current and coarse sand bottom. Benthic fauna, present in rather low density, included mainly Ephemeroptera, with a few Odonata and Trichoptera.

The stunted claws and tarsi may be the results of wear and tear in older specimens, but this phenomenon is mentioned in the description, since quite a few specimens are strikingly affected.

***Coptocatus* Montandon, 1909**

The genus *Coptocatus* was recently revised by Polhemus (1986). Including the species described below, four species are known from the eastern states of Malaysia (Sabah and Sarawak).

blunt carina, posterior part of prosternum without carina. Mesosternum with a shallow median groove and a distinct xiphus on posterior margin. Metasternum anteriorly with a strongly dorsally declivent carina, posterior part flat with a short broad blunt xiphus. Abdominal sternites with large stigmata halfway of lateral third; sternites 4, 7 and 8 with small tufts of short golden hairs medially, sternite six medially produced, sternites 5-8 medially glabrous.

Legs. Fore leg with massive femur, length 6.5 mm, width 4.3 mm; suture between tibia and tarsus shallow, claw short, blunt, hardly differentiated; anterior face of tibiotarsus and femur with golden pubescence distally becoming thicker and longer and extending onto trochanter; anterior margin of femur with a median hump and a subapical tooth (fig. 7). Posterior margin of all femora with a fringe of long hairs. Middle leg and hind femur without spines. Middle and hind tibia ventrally with a thick pad of golden brown pilosity (looks like a adhesive pad; already fully developed in larva V, and partly so in larva III/IV). Middle tibia broadened apically. Hind tibia with short spines along inner and outer faces, inner (posterior) faces with a dense fringe of long swimming hairs.

Genitalia. Parameres symmetrical, bilobed, outer lobe swollen (fig. 6). Aedeagus symmetrical, basally and centrally chitinized, apically and laterally fleshy.

Comparative notes

The same size and similar anterior margin of fore femur as *C. kinabalu* D. Polhemus, also from Sabah, which has, however, the inner lobe of paramere much shorter and the lateroposterior angles of abdominal segments not distinctly indented. The other two species in the genus known from Sabah and Sarawak do not exceed 15 mm in length.

Etymology

Stereos, a greek adjective, meaning: strong, solid, cruel, refers to the size and solid build of the species.

Remark

The holotype has a case, probably of a chironomid larva on the left hemielytron against the inner embolar ridge.

Laccocoris Stål, 1856

Seven species are known from Malesia, but none has been reported from Sulawesi (La Rivers 1971). The same is true for the genus *Heleocoris* Stål with six Malesian species. The last revision of both genera is Montandon (1897).

Laccocoris staudingeri Montandon

Laccocoris staudingeri Montandon, 1897: 440-442.

Material. – Malaysia. S. Sabah, Long Pasia area, Sg. Ritan, 4°24'N 115°42'E, 1160 m asl. Leg. J. Huisman & J. van Tol, 1 ♂ 1 ♀ (RMNH).

Distribution. – Brunei and Sabah.

Remarks. – *L. staudingeri* differs from related species in northern Borneo, *L. horvathi* Mont. and *L. maai* La Rivers (La Rivers 1970) by having the interoculus at halfway level slightly more than twice as wide as an eye.

Naucoris Fabricius, 1775

There are six Malesian species, of which one occurs in Sulawesi. A revision of the genus is not available.

Naucoris scutellaris Stål

Naucoris scutellaris Stål, 1859: 266. – Lundblad 1933a: 63-67, fig. 19 (redescription).

Material. – Sulawesi Tenggara: Kendari, N8904, 1 ♂; Mowewe, N8922A, 4 ♂ 2 ♀; 20 km S Pomalaa, N8928 (NC).

Remarks. – A widespread species, occurring from India through Sri Lanka and Thailand to Jawa and Sulawesi. The femur is strongly expanded at its inner apical two-thirds, giving the inner margin a deeply dented appearance. Other congeneric species have the inner margin of fore femur more or less straight.

NEPIDAE

Key to Indonesian and Eastern Malaysian genera

1. Flattened species, parasternites of abdomen visible, head distinctly narrower than the pronotum and partly enclosed by its anterolateral angles (Nepinae) 2
- Subcylindrical species, parasternites not visible, head free from pronotum and both of subequal width (Ranatrinae) 3
2. Respiratory siphon longer than the inner margin of the hemielytra *Laccotrephes* Stål
- Respiratory siphon not more than half as long as the distance between apex of scutellum and the membrane along inner margin of hemielytra (only one very rare species, *T. breddini* Montandon, from Northern Borneo) *Telmatotrephes* Stål

3. Eyes in lateral view globose, not reflexed downwards and not obscuring ventral margin of head *Ranatra* Fabricius
- Eyes in lateral view reflexed downwards, obscuring ventral margin of head
..... *Cercotmetus* Amyot & Serville

Laccotrephes Stål, 1865

About eight species recorded from Malesia. A generic revision is not available and the status of many species is uncertain, which makes some records unreliable. Three species are known from Sulawesi and Pulau Buton.

Key to *Laccotrephes* of Sulawesi and Buton

1. Body length over 35 mm, usually 40 mm or more *L. robustus* Stål
- Body length less than 35 mm 2
2. Respiratory siphon as long as or somewhat shorter than body *L. occultus* Lundblad
- Respiratory siphon distinctly longer than body *L. tristis* (Stål)

Laccotrephes occultus Lundblad

Laccotrephes occultus Lundblad 1933a: 23-26, fig. 2, tab. 14 (1) [nom. nov. for *L. fuscus* auctores, nec. L., redescription].

Material. – P. Buton: 16 km E of Baubau, N8944, 1 ♂ (NC). Maluku: Bacan, Wayauna, c. 50 m alt., logged forest, hand coll., 23-26 Jun 1985, leg. J. Huijbregts, 2 ♀ (RMNH).

Distribution. – Sumatera, Borneo, Buton, and Maluku (Moluccas).

Laccotrephes robustus Stål

Laccotrephes robustus Stål, 1870: 706. – Lundblad, 1933a: 26-27, fig. 3 [redescription].

Material. – Jawa: Preanger, 1 ♂ 1 ♀; Paluabuan, 3.XI.1911, 1 ♂. Sumba: Kananggar, 700 m, V.1925, 1 ♂; Mao Marroe, 450 m, V.1925, leg. Dammerman, 1 ♀. Malaysia (Sabah): Danum valley, 4°48'N 117°48'E, 220 m streamlet, 23.III.1987, leg. J. Huisman, 1 ♀ (all RMNH).

Distribution. – Widespread species: Indochina and Taiwan, Philippines, Malacca, Sumatera, Jawa, Borneo, Sulawesi, Sumba and Bali.

Laccotrephes tristis (Stål)

Nepa tristis Stål, 1854: 11.

Laccotrephes tristis; Hale, 1924: 504-507, pl. 34 (figs. 1-3), pl. 35 (figs. 2, 4, 6), pl. 36 (fig. 18); Lundblad 1933a: 25; Lansbury 1967: 644-646 [description of male genitalia].

Material. – Sulawesi Utara: Dumoga Bone N. P., Toraut, c. 200 m, multistr. evergreen forest, creek, 23.V.1985, leg. J. Huijbregts, 1 ♀ (RMNH).

Distribution. – Previously only known from Australia and New Guinea.

Remarks. – Identification of this specimen is doubtful. It differs from typical *L. occultus* by its slightly greater size (34 *vs.* 31-32 mm), its narrower appearance anteriorly (only visible under direct comparison), and its much longer respiratory siphon (40 *vs.* 30 mm).

Cercotmetus Amyot & Serville

In the excellent revision of the genus by Lansbury (1973), six species are recorded from Malesia, including one from Sulawesi. Most species of this genus are seldomly collected and then usually only one specimen at a time. Consequently, distributional patterns of most species are poorly known.

Key to Malesian species of *Cercotmetus* (Adapted from Lansbury 1973)

1. Vertex raised between the eyes, but without a distinct tubercle 2
- Vertex with a distinct, broadly and tooth-like tubercle 4
2. Less than 43 mm long, middle femora clearly shorter than prothorax (widespread species: Sumatera, Jawa, Sarawak)
..... *C. brevipes* Montandon
- More than 47 mm long, middle femora longer than prothorax 3
3. Eyes relatively small, width of vertex halfway the inner margin of eyes about twice the width of an eye at that level, vertex with a complete circlet of hairs (Sulawesi)
..... *C. robustus* Montandon
- Eyes larger, width of vertex halfway the inner margin of eyes subequal to the width of an eye, hairs on vertex few, not forming a complete circlet posteriorly (Irian Jaya)
..... *C. dissidens* Montandon
4. Distal third of tergite 6 raised and often very hairy, apex of paramere sinuate, female operculum not or hardly reaching beyond tergite 6 (widespread, Sumatera)
..... *C. compositus* Montandon
- Distal third of tergite 6 not distinctly raised and never hairy, apex of paramere evenly curved, female operculum reaching beyond tergite 6 for about one third of its length 5
5. Along median line length of anterior lobe (anterior to transverse grooves) of pronotum less than three times the length of posterior lobe (widespread, Sumatra, Jawa, Borneo)
..... *C. asiaticus* Amyot & Serville

- Along median line length of anterior lobe more than three times the length of posterior lobe (Kalimantan, Sarawak)
..... *C. asiaticus* var. *longicollis* Montandon

Cercotmetus robustus Montandon

Cercotmetus robustus Montandon, 1911: 92-93. - Lansbury 1973: 95-97, figs. 36-42 [redescription].

Material. - Sulawesi Tenggara: N8922A, 2 ♀ (NC).

Remarks. - Apparently a rare species, only known from the female holotype from Central Sulawesi ('Posso See' = Danau Poso) so far. Several small larvae, possibly of this species, were observed at locality N8931 (see appendix). Both larvae and adults are far better swimmers than *Ranatra*, they seem to use their fore legs for swimming.

Ranatra Fabricius, 1790

About twelve species recorded from Malesia, of which three have been reported from Sulawesi (one with two subspecies). The Oriental species have been revised by Lansbury (1972). In the following key to the Sulawesi species, also two unrecorded but widespread species that might turn up in Sulawesi, were included.

Key to *Ranatra* of Sulawesi

(Adapted from Lansbury 1972).

1. Head with prominent tubercle between eyes, metasternum emarginate (fig. 9) 2
 - Head at most only slightly raised between eyes, metasternum not emarginate 3
2. Length of respiratory siphon subequal to length of body (Sulawesi Tenggara)
..... *R. sulawesii* sp. n.
 - Length of siphon one-third of body length (not recorded from Sulawesi, but a widespread species, Indochina, Sumatera, Jawa, Nusa Tenggara) *R. parmata* Mayr
3. Width of fore femora measured from dorsal margin to apex of large tooth about the same as widest part of femora proximally 4
 - Width of fore femora measured from dorsal margin to apex of larger tooth clearly greater than widest part of fore femur proximally (endemic to Sulawesi) *R. malayana* Lundblad
4. Larger tooth of fore femora more or less equidistant between ends of femora (not recorded from Sulawesi, but a widespread species: India, Ceylon, Indochina, Sumatera, Jawa)
..... *R. varipes* Stål
 - Larger tooth of fore femora clearly nearer to distal end of femora 5

5. Third episternum with two clumps of small hairs (on each side) (endemic to Sulawesi Selatan) *R. longipes celebensis* Lansbury
 - Third episternum without clumps of small hairs (Indonesia, incl. Sulawesi Tenggara, E. Malaysia) *R. longipes longipes*

Ranatra longipes longipes Stål

Ranatra longipes Stål, 1861: 203.

Ranatra longipes longipes. - Lansbury 1972: 332-334, figs. 220-229 [redescription].

Material. - Sulawesi Tenggara: N8901, 3 ♂ 3 ♀; N8909, 3 ♂; N8910, 2 ♂; N8917, 2 ♂; N8919, 1 ♂ 3 ♀; N8930, 1 ♀.

Distribution. - Known from Sumatera, Borneo (Brunei, Sabah), Jawa, Bali and Sulawesi.

Remarks. - Our specimens were compared with a series from Bali, of which several were identified by Lansbury. The specimens mentioned above do not show any of the diagnostic characters characterizing subspecies *celebensis* (Lansbury 1972).

Ranatra malayana Lundblad

Ranatra birói var. *malayana* Lundblad, 1933a: 40, fig. 9A. *Ranatra malayana*. - Lansbury 1972: 319-321, figs. 142-152.

Material. - Sulawesi Tenggara: N8917, 1 ♂ 1 ♀ (NC).

Remarks. - Until now only known by three specimens from Sulawesi Selatan. Respiratory siphon, when folded back over dorsum, reaching halfway head in the male, and anterior margin of pronotum in female.

Ranatra sulawesii sp. n.

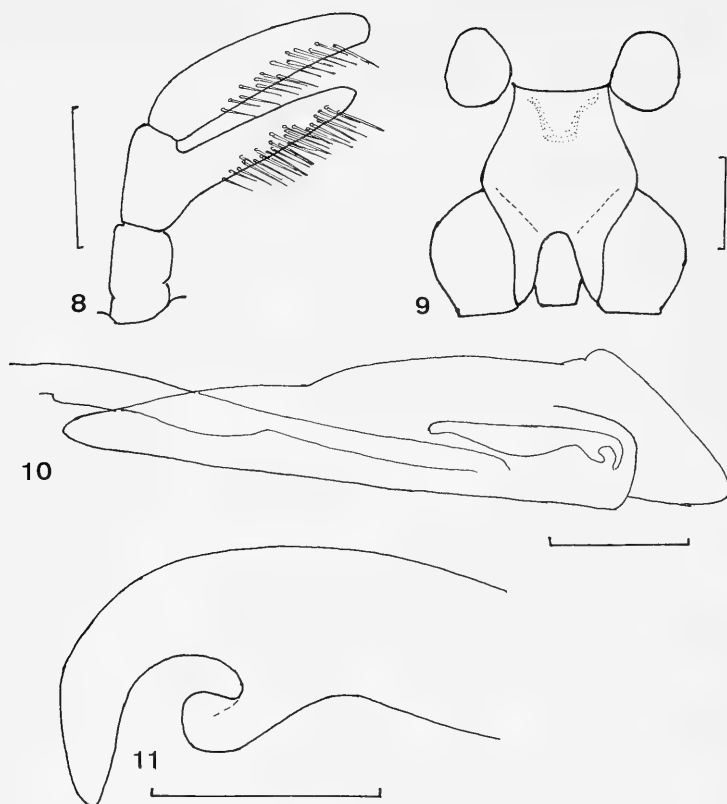
(figs. 8-11)

Type material. - Holotype ♂: Sulawesi Tenggara, K. Kendari, pond with *Nymphaea* at Wawonggole, 20.II.1989, N8902, leg. N. Nieser (RMNH). - 10 ♂ 7 ♀ (including one labelled allotype), same data as holotype, deposited as follows: 1 ♀ (RMNH); 3 ♂ 2 ♀ (NC); 1 ♂ 1 ♀ (MBBJ); 1 ♂ (BPUH); 1 ♂ 1 ♀ (JTPC); 1 ♂ 1 ♀ (SEMC); 1 ♂ (OXUM).

Description

Adult. - Measurements. Length ♂ 34-38.3 mm; ♀ 35-39.5 mm; length of siphon ♂ 39.0-41.7 mm, ♀ 35-45 mm; width of head ♂ 3.2-3.3 mm, ♀ 3.2-3.5 mm; humeral width of pronotum ♂ 3.5-3.9 mm; ♀ 3.6-4.2 mm. Colour. Dark brown, legs paler with indistinct annulation.

Figs. 8-11. *Ranatra sulawesii*. – 8, antenna; 9, metasternum, 10, genital capsule of male, lateral view; 11, apex of paramere. Scales: 0.5 mm (8), 1 mm (9-10), 0.25 mm (11).



Head with small, but distinct nodule on vertex; eyes slightly wider than width of interoculus; lora strongly developed, higher than clypeus, which has two small nodules apically; second segment of antennae with long, finger-like projection, subequal to length of segment 3 (fig. 8).

Thorax. Prothorax in lateral view about $1.5 \times$ as long as fore coxa, about $1.1 \times$ as long as fore femur; anterior lobe twice as long as posterior lobe in median line; anterior margin not conspicuously raised; humeral width / anterior width 1.4 ; pronotal grooves well developed; posterior lobe without tubercles, ventrally with a broad concavity anteriorly at insertion of coxae, caused by produced anteroventral angles, remainder of prothorax flat with a vague carina in anterior one-third. Scutellum about $1.5 \times$ longer than wide, with a shallow broad transverse depression in apical third. Mesosternum with anterior margin raised, posterior margin of metasternum deeply incised (fig. 9); space between middle and hind coxae subequal.

Legs. Fore femur with one median tooth at apical 0.4 of femoral length, no secondary tooth distally. Length of middle and hind femur subequal. Middle

tibia shorter, hind tibia longer than femur; apical $\frac{3}{4}$ of middle and hind tibia with hair fringe. Hind femur reaching about $\frac{3}{4}$ along last abdominal sternite in both sexes.

Male genitalia. See figs. 10, 11.

Female. – Genital operculum not reaching the base of respiratory siphon.

Comparative notes

Based on the tuberculate vertex and emarginate metasternum this species can be included in the *R. gracilis* group (Lansbury 1972). *R. sulawesii* can be distinguished by (a) siphon longer than the body length, (b) distance between the middle and the hind coxae subequal, and (c) finger-like projection of antennal segment 2 long. In the key by Lansbury (1972) it runs to *R. parmata* Mayr, from which it differs by its long siphon, and the shape of the paramere, which is apically more swollen in *R. parmata*.

Etymology

Sulawesii, a noun in genitive case, refers to the type locality.

Remark

The type locality is a small pond at the edge of marshy fields with some water lilies (*Nymphaea* sp.), and abundant marginal vegetation flattened and hanging into the water.

NOTONECTIDAE**Key to Indonesian and Eastern Malaysian genera**

1. Hemelytral commissure anteriorly without a definite hair-lined pit (Notonectinae) 2
- Hemelytral commissure anteriorly with a definite hair-lined pit (Anisopinae) *Anisops* Spinola
2. Middle femur with an anteapical pointed protuberance *Enithares* Spinola
- Middle femur without such a protuberance 3
3. Eyes contiguous or forming an ocular commissure near posterior border of head *Nychia* Stål
- Eyes widely spaced near posterior border of head *Apelonecta* Lansbury

***Anisops* Spinola, 1840**

Due to insufficient knowledge of the fauna, a key to the regional species of the genus *Anisops* Spinola cannot be presented. The reader is referred to Brooks' (1951) revision and various papers by Lansbury (1964, 1965, 1978). Several species, e.g. *A. breddini*, *A. nasuta* and *A. paracrinata*, can be found in village ponds and rice fields. Such species tend to be very widespread in Southeast Asia.

***Anisops batillifrons* Lundblad**

Anisops batillifrons Lundblad, 1933: 463-464, fig. 8. – Brooks 1951: 420-423, figs. 71, 101.

Material. – Malaysia, Sabah: 16 km NE Tenom: Agricultural Research Station, Sg. Segalan, 115°59'E 5°12'N, a. l., 23.XI.1987, 1 ♂ 1 ♀, leg. J. Huisman & R. de Jong (RMNH).

Distribution. – A widespread species: India through Indochina to Hainan, Taiwan, Iriomote and the Philippines; apparently mainly in subtropical regions.

***Anisops biroi* Brooks**

Anisops biroi Brooks, 1951: 454-456, fig. 49. – Lansbury 1978: 111, figs. 37-39.

Material. – Sulawesi Tengah: 50 km SE of Palu: Lore Lindu N.P., Sopa valley near Dongi Dongi, 6 Dec 1985 (sample B), leg. J. van Tol & J. Krikken 3 ♂ 2 ♀ (RMNH). Pulau Buton: N8939, 10 ♂ 4 ♀ (NC). Maluku: Bacan, Wayauna, alt. 50 m, sec. growth, eutrophic pool, 5-7 July 1985, HH382, leg. J. Huijbregts, 1 ♂ 5 ♀ (RMNH).

Remarks. – Identification of this species somewhat doubtful. The rather short rostral prong suggests the very similar *A. rigoensis*. None of the present specimens, however, has a carina on the posterior part of the vertex, which is reported to be characteristic for *A. rigoensis* (Lansbury 1978). Both species were only known from New Guinea up to now.

***Anisops breddini* Kirkaldy**

Anisops breddini Kirkaldy, 1901a: 5-6. – Brooks 1951: 439-441, figs. 78, 99; Leong 1962 [life cycle]; Lansbury 1965: 58.

Material. – Sulawesi Tenggara: N8901, 22 ♂ 27 ♀, 5 larvae; N8917, 1 ♂ 1 ♀; N8918, 1 ♂ 1 ♀; N8931, 1 ♂ 1 ♀. Pulau Buton, N8938, 5 ♂ 22 ♀.

Distribution. – Widespread species: India and Sri Lanka through Indochina to Jawa, Sulawesi and Buton.

***Anisops nasuta* Fieber**

Anisops nasuta Fieber, 1851: 484-485. – Lundblad 1933a: 168-171, fig. 58; Brooks 1951: 416-418, figs. 60, 98; Lansbury 1965: 61.

Material. – Sulawesi Tenggara: N8917, 4 ♂ 4 ♀ 31 larvae; N8931, 3 ♂ 5 ♀. Pulau Buton: N8938, 16 ♂ 21 ♀.

Distribution. – A very widespread species: E. India and Sri Lanka through China and Indonesia to Australia and Samoa.

***Anisops occipitalis* Breddin**

Anisops occipitalis Breddin, 1905: 152. – Brooks 1951: 344-346, fig. 22; Lansbury 1965: 61-67, figs. 3-4, 7-8.

Material. – Sulawesi Tenggara. N8908, 8 ♂ 15 ♀; N8917, 2 ♂; N8927, 4 ♂ 7 ♀; N8931, 1 ♂ 1 ♀. Pulau Buton. N8938, 1 ♂ 1 ♀.

Distribution. – Widespread through Indonesia to Northern Australia.

***Anisops paracrinata* Brooks**

Anisops paracrinata Brooks 1951: 329-331, fig. 12. – Lansbury 1965: 57-58.

Material. – Sulawesi Tengah. SW of Luwuk, Totop camp along Batui River, 19-21 Oct 1989, Sul. 18, J. P. Duffels, 1 ♂ (ZMA). Sulawesi Tenggara. Desa Kagunyal, N8908, 1 ♂ 6 ♀; Jalan Asera, N8917, 26 ♂ 23 ♀; Jalan Asera, N8918, 5 ♂ 1 ♀; 20 km S Pomalaa, N8927, 4 ♂; 15 km S Pomalaa, N8931, 17 ♂ 17 ♀. Pulau Buton. Desa Gareg-Gareng, N8938, 36 ♂ ∞ ♀.

Distribution. – Sumatera, Jawa, Bali, Sumbawa, Sulawesi, Buton, E. Australia.

Anisops stali Kirkaldy

Anisops stali Kirkaldy, 1904: 113, 132. – Brooks 1951: 319-322, figs. 9, 107; Lansbury 1965: 58.

Material. – Sulawesi Tenggara. Desa Kagunyal, N8908, 2 ♀; 15 km S Pomalaa, N8931, 2 ♀.

Remark. – Identification of these specimens uncertain since no males were available; they agree with specimens from Jawa.

Distribution. – Widespread; the Philippines, Jawa, Sulawesi, Nusa Tenggara, Australia, Okinawa.

Anisops tabitiensis Lundblad

Anisops tabitiensis Lundblad, 1934: 121-123, figs. 1-5. – Brooks 1951: 376-378, fig. 40; Lansbury 1964: 217-218, fig. 7.

Material. – Sulawesi Tenggara. 20 km E Kolaka, N8934, 4 ♂. Malaysia, Sabah. 20 km W of Sandakan, Sepilok-Laut. ML, 4 Nov. 1987, leg. J. Huisman & R. de Jong, 1 ♂ (RMNH).

Remark. – The specimens were compared with a male from New Guinea and they differ only in the facial carina being slightly less prominent in the Sulawesi and Sabah specimens.

Distribution. – Widespread: Andaman Islands, Borneo, Sulawesi, the Philippines, New Guinea, New Hebrides, Tahiti, Guadalcanal, Okinawa.

Abelonecta Lansbury

This genus contains three species, one from Thailand and two from Borneo (Lansbury 1966).

Abelonecta alexis Lansbury

Abelonecta alexis Lansbury, 1965a: 328-330, figs. 2-18. – Lansbury 1966: 632.

Material. – Malaysia, Sabah. 60 km W of Lahad Datu, Danum Valley, 14 Mar 1987 (B), leg. J. Huisman, 1 ♂ (RMNH).

Distribution. – Sabah and Sarawak.

Enithares Spinola

A large, mostly Oriental genus. Thirty-three species are known from Malesia, of which seven occur in Sulawesi and one on Buton. There is an excellent revision of the Oriental species (Lansbury 1968).

Key to the males of *Enithares* of Sulawesi and Buton

1. Embolium in ventral view (ventral ridge of hemielytron) greatly expanded anteriorly (fig. 21); pronotal humeral angles produced into broad knobs. Length about 9 mm (Sulawesi) *E. producta* Lsb.
- Embolium in ventral view not greatly expanded anteriorly; pronotal humeral angles not produced 2
2. Length up to 9 mm 3
- Length 9.5 mm or more 4
3. Head width twice the median length or less, anterior lobe of genital capsule bilobed due to a deep and broad median incision (widespread species) *E. bakeri* Brks.
- Head width just over twice its median length, anterior lobe of genital capsule not bilobed (P. Biak, possibly Sulawesi Tenggara) *E. vulgaris* Lsb.
4. Length 12.5 mm, median length of head one-fourth of its length shorter than median length of pronotum, anterior margin of middle tibia straight to very slightly concave, posterior lobe of genital capsule broadly rodlike (Sulawesi Selatan) *E. horvathi* Kirk.
- Length not over 12 mm; if apex of posterior lobe of genital capsule rodlike, then length not over 11 mm, anterior margin of middle tibia more or less convex 5
5. Apex of posterior lobe of genital capsule rodlike (figs. 13, 16) 6
- Apex of posterior lobe of genital capsule rounded (figs. 12, 15) 7
6. Middle tibia not distinctly broadened (fig. 18), rod-like apices of posterior lobes of genital capsule rather short with small solid pegs on inner sides (fig. 13) (Sulawesi Tenggara) *E. lansburyi* sp. n.
- Middle tibia distinctly broadened (fig. 20), rod-like apices of posterior lobes of genital capsule more elongate without pegs on inner sides (fig. 16) (P. Buton) *E. skutalis* sp. n.
7. Apical half of middle femora with very long hairs, covering ventral margin in inner view; genital capsule with a bilobed posterior lobe bearing an apicaudal tuft of setae (fig. 12) (Sulawesi Tengah) *E. caesaris* sp. n.
- Middle femora without strikingly long hairs,

posterior lobe of genital capsule not bilobed,
without tuft of setae (fig. 15)
..... *E. phenakismos* sp. n.

Enithares bakeri Brooks

Enithares bakeri Brooks, 1948: 40, pl. 1, fig. 3. – Lansbury 1968: 384-385, figs. 91-95; Nieser & Chen, in press.

Material. – Sulawesi Tenggara. Desa Kagunya, N8908, 1 ♂ 1 ♀; Aopa marsh, N8913, 1 ♀; Jalan Asera, N8917, 1 ♂; 15 km S Pomalaa, N8931, 4 ♀. Pulau Buton. Desa Gareg-Gareg, N8938, 1 ♂ 1 ♀. Maluku. Bacan, Wayaua, eutrophic pool, HH382, 6-7 July 1985, leg. J. Huijbregts, 2 ♂ 3 ♀ (RMNH).

Distribution. – One of the few widespread species of *Enithares* in the area, occurring in the Philippines, Sabah, Sulawesi, Maluku, Flores.

Remarks. – The length of the females from Sulawesi and Buton centers around 7.5 mm, which is slightly less, and of the specimens from the Maluku around 8.3, which is slightly more than indicated by Lansbury (1968). This suggests that the variability in size is greater than known up to now, and that there is significant variability between populations.

Enithares bakeri is smaller than most of its congeners, and lives e.g. in village ponds together with the more common species of *Anisops*.

Enithares bippokleides Kirkaldy

Enithares bippokleides Kirkaldy, 1898: 73. – Lansbury 1968: 400-402, figs. 165-172 [redescription, synonymy].

Material. – Jawa, S. Muller [19th century], 1 ♂ 2 ♀; G. Malang, Aug. 1935, 4 ♂ 2 ♀ (all det. *E. fruhstorferi* by Brooks) (RMNH).

Distribution. – Only known from Jawa.

Enithares intricata Breddin

Enithares intricata Breddin, 1905: 154. – Lundblad 1933a: 174-177, fig. 64, pl. 5, 21; Lansbury 1968: 404-405, figs. 185-190 [redescription, synonymy].

Material. – N. Sumatra: Toba plateau, Tigadolok, 2°50'N 99°03'E, c. 150 m, 20 Jun 1972, leg. J. Krieken (21), 1 ♀ (RMNH).

Distribution. – Sumatera and Jawa.

Enithares producta Lansbury

Enithares producta Lansbury, 1968: 368-369, figs. 15-21.

Material. – Sulawesi Utara: Dumoga Bone N. P., several localities, incl. Tumpah river, Toraut river, Waterfall Creek, small creek near basecamp, leg. J. P. Duffels, J. Huijbregts, J. van Tol, total 13 ♂ 14 ♀ (ZMA, RMNH). Sulawesi Tengah. 60 km SE Palu: Lore Lindu NP, Danau Taming and brooklets, 1600 m, 7 Dec 1985, leg. J. van Tol, 1 ♀ (RMNH).

Distribution. – Sulawesi.

Enithares riplejana Lansbury

Enithares riplejana Lansbury, 1968: 402-403, figs. 173-178.

Material. – Maluku. Bacan. Wayaua, logged forest, 5-16 July 1985, leg. J. Huijbregts, 1 ♂ (NC).

Distribution. – Bacan, which is the present spelling of Batjan, the type locality of this species.

Remarks. – This specimen agrees with the description of *E. riplejana*, except for its smaller size (7.3 mm), and the apical part of the posterior lobe of the genital capsule, which is inclined caudad. The dense tuft of setae on the genital capsule look solid when glued dry on a card.

Enithares vulgaris Lansbury

Enithares vulgaris Lansbury, 1968: 403-404.

Material. – Sulawesi Tenggara. 20 km E Kolaka, N8934, 1 ♀.

Distribution. – So far only known from the type series from P. Biak, situated east from the NW part of Irian Jaya.

Remarks. – The size of the Sulawesi specimen is 9.1 mm, which indicates to *E. vulgaris* rather than to *E. intricata* Breddin. Males are needed for definitive identification.

Enithares caesaries sp. n.

(Figs. 12, 17)

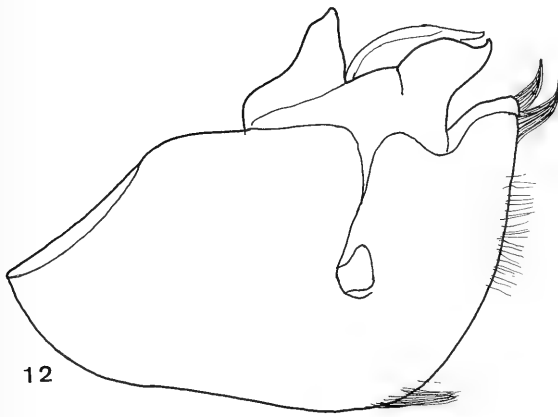
Type material. – Holotype ♂: Sulawesi Tengah. Luwuk area, Sungai Tikalalang, 20 Oct 1989, 89JvT26, leg. J. van Tol (RMNH).

Description

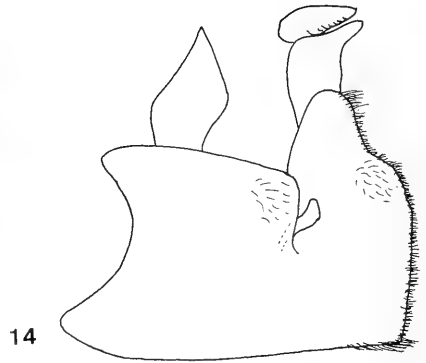
The description is based on the holotype only. Generally a rather large boat-shaped species, greatest width at level of apex of scutellum.

Measurements. – Length 10.3 mm, maximal width 4.03 mm, width of head 3.22 mm, humeral width of pronotum 3.81 mm, anterior width of vertex 1.10 mm, synthipsis 0.70 mm.

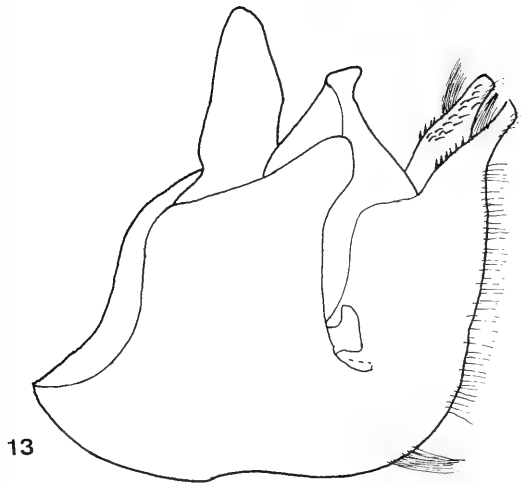
Colour. – Pale luteous, eyes dark brown, apical



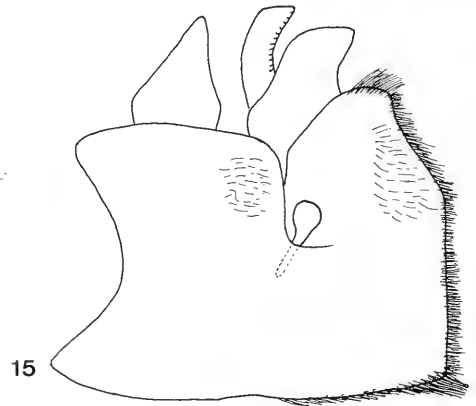
12



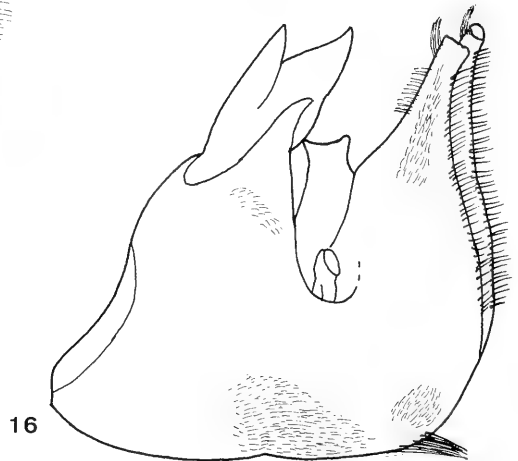
14



13



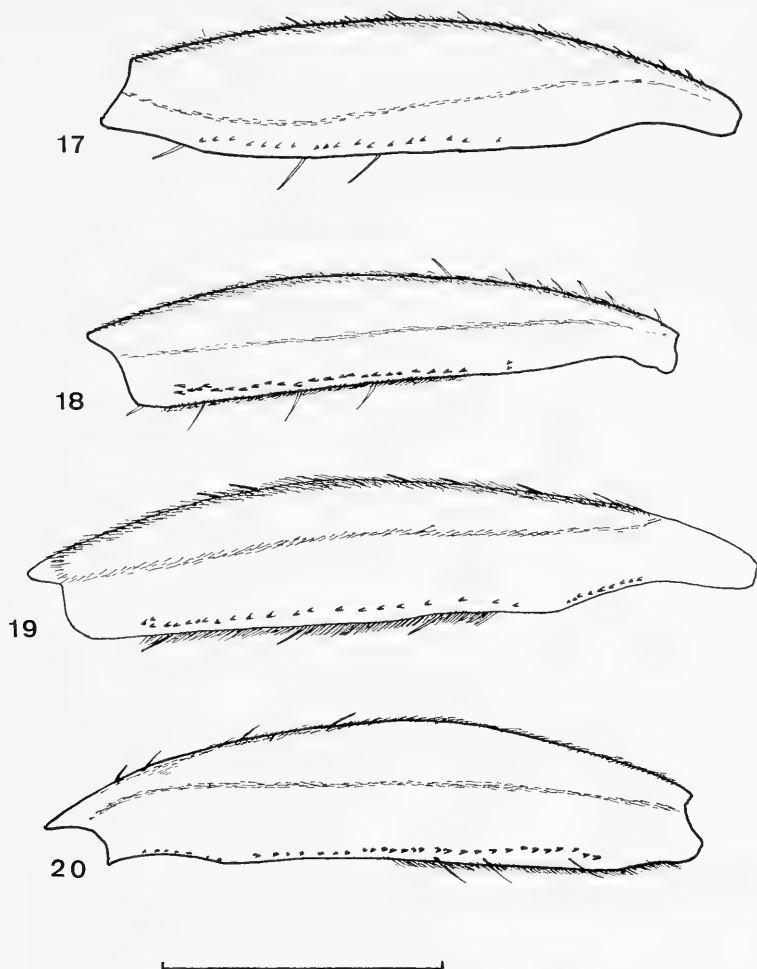
15



16



Figs. 12-16. Genital capsule in male *Enitbares*. – 12, *E. caesaries*, holotype; 13, *E. lansburyi*, paratype; 14, *E. hipokleides*; 15, *E. phenakismos*, holotype; 16, *E. skutalis*, paratype. Scale bar 1 mm.



Figs. 17-20. Middle tibia of male *Enithares*. 17, *E. caesaries*, holotype; 18, *E. lansburyi*, paratype; 19, *E. phenakismos*, holotype; 20, *E. skutalis*, paratype. Scale bar 1 mm.

half of membrane smoky brown to blackish. Ventral side pale with rostrum, stripe along inner (costal) margin of embolium, pilosity, spines, patches and stripes dark brown to blackish.

Head and thorax. – Anterior margin of vertex in dorsal view truncate, hardly produced anterior to eyes. Greatest width of head $2.3 \times$ its median length; median length of head and median length of pronotum subequal, somewhat longer than anterior width of vertex. Humeral width of pronotum $3 \times$ its median length, lateral margin slightly diverging, posterior margin somewhat sinuate. Dorsal margin of pronotal fovea slightly diverging behind eyes. Embolium only slightly expanded in anterior third. Nodal furrow about its own length from membranal suture.

Legs. – Fore trochanter narrow posteriorly, with some long hairs, without nodule on ventral side,

meso-trochanter rounded. Mid-femoral hairs in apical half very long, covering ventral margin in inner view; mid tibia not broadened, slightly convex along anterior margin (fig. 17), outer claw of midleg normal.

Ventral side. – Lateral edges of metaxiphus only slightly rounded and thickened, apical part with sinuate margins resulting in a sharply projecting apex. Connexiva of segments 1-3 with small black spines, not ridged.

Male genitalia. – Genital capsule as in fig. 12; posterior lobe strongly sclerotized, its dorsal margin incised, the distal top with a distinct tuft of hairs; anterior lobe less sclerotized, parameres very small, set in depressions in sides of capsule.

Comparative notes

In the key by Lansbury (1968) this species runs

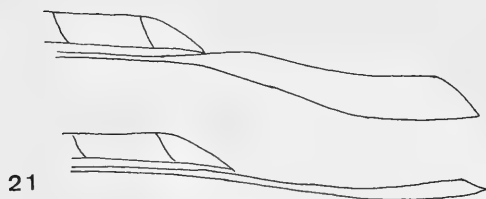


Fig. 21. Base of hemielytra and connexiva in *Enithares*, semidiagrammatical, in ventral view. Upper: greatly expanded anteriorly (as in *E. producta*), lower: not expanded.

to *E. alexis* Lansb. in view of the midfemoral hairs, or, ignoring this character, to *E. hippokleides* Kirk. or *E. timorensis* Brooks. The last two species lack the midfemoral hairs, have also the middle tibia less hairy and the dorsal margin of the hindlobe of the genital capsule not incised. This species is also quite similar to *E. lansburyi* sp. n. (see the key).

Etymology

Caesaries (Latin: thick strands of hair), a noun in apposition, refers to the pilosity of the middle femur.

Enithares lansburyi sp. n. (figs 13, 18)

Type material. – Holotype ♂: Sulawesi Tenggara, small mountain stream 20 km E of Kolaka, N8934, 3 March 1989, leg. N. Nieser (ZMA). – Paratypes: 1 ♀ (ZMA); 3 ♂ 3 ♀ (allotype) (NC, 1 ♂ MBBJ).

Description

Shape. – Rather large boat-shaped species, greatest width over pronotal humeral angles.

Measurements. – Length ♂ 9.4–10.1 mm, ♀ 9.2–10.0 mm; maximal width 3.7–3.9 mm; width of head 3.0–3.1 mm; humeral width of pronotum 3.7–3.9 mm; anterior width of vertex 1.0–1.1 mm; synthipsis 0.61–0.69 mm.

Colour. – Pale form: Pale luteous, eyes dark brown, apical half of membrane and a large x-shaped spot at apex of scutellum smoky brown to blackish. Ventral side pale with proximal part of embolium, pilosity, spines, patches and stripes blackish. Dark form: anterior fourth of pronotum smoky brown, scutellum shiny black with, in fresh specimens, light greenish somewhat fluorescent stripes along lateral margins, in dried specimens these stripes become pale luteous. Hemielytra hyaline with apex of clavus, inner angle and outer band of corium and basal part of membrane black. Dorsum of abdomen black, showing through hyaline

parts of hemielytra.

Head and thorax. – Anterior margin of vertex in dorsal view truncate, slightly produced anterior to eyes. Greatest width of head 2.5 times its median length in male, just over two times its length in female; median length of head and median length of pronotum subequal, somewhat longer than anterior width of vertex. Humeral width of pronotum just under three times its median length, lateral margins slightly diverging, posterior margin shallowly sinuate. Dorsal margin of pronotal fovea slightly diverging behind eyes. Embolium only slightly expanded in anterior third. Nodal furrow virtually straight with tip inclined cephalad, slightly less than its own length removed from membranal suture in male, distance and length subequal in female. Legs. – Fore trochanter narrow posteriorly, with some long hairs, without nodule ventrally, middle trochanter rounded. Male middle tibia not broadened, slightly convex along anterior margin (fig. 18), outer claw of middle leg normal.

Venter. – Metaxiphus with rounded and thickened lateral edges, apical part with sinuate margins resulting in a sharply projecting apex. Connexiva, segments 1 and 2 with small spines, not ridged.

Male genitalia. – Genital capsule as in fig. 13, posterior lobe strongly sclerotized, long and stylus-like distally, the distal part with hairs and apically some spines, mainly located on the inner faces. Anterior lobe less sclerotized, parameres very small, set in depressions in sides of capsule.

Comparative notes

In the key by Lansbury (1968) this species runs to *E. hippokleides* Kirk., which lacks the elongate stylus-like apices of the hind lobes of the genital capsule. *E. lansburyi* is very similar to *E. skutalis*, but differs in the apex of the metaxiphus, which is more pronounced, and in the characters mentioned in the key.

Etymology

Named in honour of Dr. I. Lansbury for his excellent work on this genus and other Oriental Notonectidae.

Biological notes

E. lansburyi and *E. skutalis* were found in similar habitats, virtually stagnant, shaded pools associated with small streams in woodland. In each pool one or two specimens can be found, while larvae, especially the smaller ones, may be found in larger numbers and are of the same or of consecutive instars. We hypothesize, that gravid *Enithares* females seek out suitable ponds to deposit a number of eggs. The larvae start to use other kind of food,

but in the end, when supplies become exhausted, resort to cannibalism. In this way the species stores the energy to produce a few adults temporarily in the larval population, which is also known in several species of *Notonecta*.

***Enithares phenakismos* sp. n.**
(Figs. 15, 19)

Material. – Holotype ♂: Sulawesi Tengah: Lore Lindu National Park, 10 km NE Gimpu, lower montane forest, Rano Rano, 1600 m, 15 Mar 1985, Sta. 42, J. P. Duffels & M. J. Duffels (ZMA).

Description

Only the holotype is known. Rather large boat-shaped species, greatest width probably at a level halfway scutellum (in the type right hemielytron somewhat broken and folded outward).

Male. – Measurements. Length 11.9 mm, width of head 3.72 mm, humeral width of pronotum 4.3 mm, anterior width of vertex 1.40 mm, synthlipsis 0.98 mm.

Colour. Pale luteous, eyes black, vertex light brownish, dark spot on abdominal dorsum at apices of clavi shining through hemielytra, which are opaque except for apical, hyaline half of membrane. Ventrally pale with stripes, pilosity and spines mostly dark brown to blackish.

Head and thorax. Anterior margin of vertex in dorsal view rounded, hardly produced anterior of eyes. Greatest width of head twice its median length; median length of head and median length of pronotum subequal, only slightly longer than anterior width of vertex. Humeral width of pronotum three times its median length, lateral margins slightly diverging, posterior margin nearly straight in median part, gently curved anteriorly in lateral parts. Dorsal margin of pronotal fovea converging behind eyes. Embolus only slightly expanded in anterior third. Nodal furrow about its own length removed from membranal suture.

Legs. Fore trochanter posteriorly narrow, with some long hairs, without nodule ventrally, mesotrochanter rounded. Mid-femoral hairs normal, with a row of short black hairs near suture with trochanter, but lacking the small patch of short black bristles at its apex, which are visible in most specimens of *E. hippokleides*, middle tibia not broadened, slightly convex along anterior margin (fig. 19), outer claw of middle leg normal.

Venter. Sides of metaxiphus somewhat rounded and thicken, apex long and sharply projecting. Connexiva of segments 1–3 with small black spines, not ridged.

Genital capsule as in fig. 15, posterior lobe with sinuate posterior margin.

Comparative notes

This species runs to *E. hippokleides* Kirk. in the key by Lansbury (1968). At first sight it looks like an oversized specimen of *E. hippokleides*, including a similarity of the genital capsule and the pilosity of the legs. On closer inspection there are several small structural differences, viz. head width / synthlipsis about 6 in *E. hippokleides* and less than 4 in *E. phenakismos*, anterior width vertex / synthlipsis about 2 in *E. hippokleides* and 1.5 in *E. phenakismos*, dorsal margin of pronotal fovea slightly diverging posteriorly in *E. hippokleides* and converging in *E. phenakismos*, apex of metaxiphus longer in *E. phenakismos* than in *E. hippokleides*. Characters to distinguish *E. phenakismos* from other new species described in this paper can be found in the key. *E. timorensis* Brooks, which is considered to be closely related to *E. hippokleides*, is even smaller (length of male up to 9.5 mm) and has the posterior lobe of the genital capsule not sinuate.

Etymology

Phenakismos (Gr. deceit), a noun in apposition, refers to the close similarity to *E. hippokleides* Kirk.

***Enithares skutalis* sp. n.**
(figs. 16, 20)

Type material. – Holotype ♂: Pulau Buton, 16 km E Baubau, small stream in wet forest, 10.III.1989, N8944, leg. N. Nieser (ZMA). – Paratypes: 1 ♂ with same data as holotype (NC); Buton, small mountain stream, N8941, 2 ♂ (NC), 1 ♂ (MBJ).

Description

Male. – Shape. Rather large, boat-shaped species, greatest width across hemielytra just behind pronotal humeral angles.

Measurements. Length 10.4–10.8 mm, maximal width 4.10–4.15 mm, width of head 3.25 mm, humeral width of pronotum 4.00–4.05 mm, anterior width of vertex 1.15–1.20 mm, synthlipsis 0.65–0.68 mm.

Colour. Pale luteous, eyes dark brown, apical half of membrane smoky brown, spot just caudally of scutellum light smoky brown. Ventral side pale with pilosity, spines, patches and stripes blackish.

Head and thorax. Anterior margin of head in dorsal view nearly straight. Greatest width of head $2.5 \times$ its median length; median length of head, median length of pronotum and anterior width of vertex subequal. Humeral width of pronotum more than $3 \times$ its median length. Pronotum with lateral margins diverging, posterior margin straight; dor-

sal margin of pronotal fovea directed virtually straight caudad behind eyes. Embolium only slightly expanded in anterior third. Nodal furrow virtually straight with tip inclined cephalad, slightly less than its own length removed from membranous suture.

Legs. Fore trochanter narrow posteriorly, covered with thick long hairs, without nodule ventrally, mesotrochanter rounded. Male middle tibia slightly broadened, convex along anterior margin (fig. 20), outer claw of middle leg normal.

Venter. Metaxiphus with distinct rounded and thickened lateral edges, apical part triangular with virtually straight lateral margins. Connexiva of segments 1 and 2 with small black spines, not ridged.

Genital capsule as in fig. 16, posterior lobe strongly sclerotized, long, hairy and distally stylus-like. Anterior lobe less sclerotized, parameres very small, set in depressions in sides of capsule.

Comparative notes

This species runs to *E. hebridensis* Lansb. or *E. hippokleides* Kirk. in the key by Lansbury (1968), which, however, both lack the elongate stylus-like apex of the hind lobe of the genital capsule, and differ in the shape of the male middle tibia. The genital capsule of *E. skutalis* has a structure similar to *E. horvathi* and *E. lansburyi*, but in detail these are quite different. Besides, *E. horvathi* is two mm longer and has the anterior margin of the male middle tibia slightly concave (convex in *E. skutalis*).

Etymology

Skutalis (Gr. baton), a noun in apposition, refers to the rodlike shape of the apex of the posterior lobe of the genital capsule.

Nychia Stål

Genus with only a few, mostly poorly known species. Apparently only one species in Malesia (Lansbury 1985).

Nychia sappho Kirkaldy

Nychia marshalli var. *sappho* Kirkaldy, 1901a: 809-810. *Nychia malayana* Lundblad, 1933a: 148-155, figs. 49-51. *Nychia sappho*; Lansbury 1985: 4-8, figs. 7-21.

Material. – Sulawesi Tenggara: Wawangole, N8901, 2 ♂ 4 ♀; Sungai Sampara, N8909, 3 ♂ 3 ♀; 2 km E Sungai Sampara, N8910, 1 ♀; Aopa marsh, N8913, 7 ♂ 3 ♀; Jalan Asera, N8916, 1 ♀. Pulau Buton: Road to Lawele, N8939, 5 ♂ 5 ♀, all brachypterous.

Distribution. – Malaysia, Indonesia, New Guinea and Northern Australia.

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APPENDIX 1

Localities sampled by N. Nieser, Indonesia, Sulawesi Tenggara, 1989.

- N8901-N8920: **Kabupaten Kendari**
 N8901-N8902: *Kecamatan Wawotobi*
 N8901. Wawonggole, Sungai Anggoro, 20 Feb. 1989. Quietly flowing stream in open woodland, width 4-5 m, depth up to 1 m, dark brown water; vegetation hanging from the banks in the water.
- N8902. Wawongole. 20 Feb. 1989. Pond with abundant *Nymphaea* in marshy fields; shore vegetation hanging into the water.
- N8903-N8912: *Kecamatan Kendari*
 N8903. Eastern road to Lalimboe, 3 km outside Kendari, 21 Feb. 1989. Small stream, width 2-3 m, current 15m/m, slower in ponded sites, bottom sandy, some detergents, but clear.
- N8903A. Same site, puddle at edge.
- N8904. Eastern road to Lalimboe, 4 km outside Kendari, 21 Feb. 1989. Turbid, near stagnant stream, width 1.5 m, depth up to 1 m.
- N8905. Desa Kagunya, 21 Feb. 1989. Trench.
- N8906. Desa Kagunya, 21 Feb. 1989. Pond covered with *Azolla* and *Lemna*. 100 × 10 m, depth 0.05 m, bottom clay and mud.
- N8907. Desa Kagunya, 21 Feb. 1989. Pond with some *Lemna*, 15 × 5 m, depth 0.05 m, bottom clay and mud.
- N8908. Road outside Desa Kagunya, 21 Feb. 1989. Pond, 100 × 50 m, turbid, beige, grass-like vegetation along one bank. Many *Cybister* and *Dytiscus*.
- N8909. Sungai Sampara, second bridge along road Kendari-Wawotobi, 22 Feb. 1989. River, sampled along bank at bridge, water turbid, beige, sand bottom.
- N8910. About 2 km E of N8909, 22 Feb. 1989. Puddle in dry stream bed in savannah-like area at foot of hill with monsoon forest.
- N8911. Small stream about 8 km E of N8909, 22 Feb. 1989. Width 3 m, depth 0.6 m, water turbid, beige, bottom sand and loam. Current up to 5 m/min.
- N8912. Puddle high on banks of N8911, 22 Feb. 1989. Dimensions 10 × 3 m, depth 0.4 m.
- N8913-N8915: *Kecamatan Lembuya*
 N8913. Aopa marsh, 23 Feb. 1989. Bay in marsh at office building, grass-like vegetation on banks, *Ceratophyllum* in water, water light brown but clear.
- N8914. Road Lembuya-Palangga, desa Lamooso, 23 Feb. 1989. Sungai Simbangi. Open loamy and sand bottom. Slow current.
- N8915. Road Lembuya-Palangga, 23 Feb. 1989. Swampy banks of stream in savannah.
- N8916-N8920. *Kecamatan Asera*.
 N8916. Jalan Asera, first stream from bridge over S. Sampara, 24 Feb. 1989. Riffles with current 15-20 m/min. *Rhagovelia*.
- N8917. Pool in meadow near N8916, 24 Feb. 1989. Dimensions 4 × 2.5 m, depth up to 0.3 m, water turbid, beige, grass-like vegetation and *Polygonum*.
- N8918. Flooded banks of second stream, 24 Feb. 1989. Meadows mainly with Cyperaceae, water turbid, beige.
- N8919. Same road, but here named Jalan Paku Jaya, fifth stream at slightly higher elevation, 24 Feb. 1989. At bridge, slow current, bottom sand and clay.
- N8920. Same road, fourth stream, coming from wood-

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land, 24 Feb. 1989. *Ptilomera* in shade of trees, *Limnognonius* in exposed puddle aside of current.

N8921-N8934: Kabupaten Kolaka

N8921. Kecamatan Kolaka

N8921. Sungai Kolaka, 27 Feb. 1989. Upstream of Kolaka, river, bottom sand and pebbles, current variable. *Ochierus* and *Hydrometra* on mudflat.

N8921A. Same site, places with current.

N8921B. Same site, ponded sites.

N8922-N8924: Kecamatan Mowewe.

N8922. Sungai Mowewe, 28 Feb. 1989. Lowland stream, 2.5-10 m wide, in woodland with fields and settlements closeby. Water clear, colourless. Bottom sample at shallow, partly shaded places with moderate current, bottom coarse sand and small pebbles.

N8922A. Same site, pothole with undercut bank, tree roots, floating plant debris, depth over 1 m.

N8923. Small stream in fields and gardens near N8922, 28 Feb. 1989. Width 0.5-1 m, depth 0.1-0.3 m, bottom mostly pebbles, rather fast current.

N8924. Puddles on path at N8922-N8923, 28 Feb. 1989.

N8925-N8931: Kecamatan Kolaka.

N8925. Tamborasi, 1 Mar. 1989. Subterranean stream flowing into small creek.

N8926. Between Tamborasi and Wolo, 1 Mar. 1989. Mountain stream through cocoa plantation. *Ptilomera* and *Rhagovelia* on more quiet sites behind boulders. *Limnognonius* on puddle on banks.

N8927. About 20 km S of Pomalaa, 2 Mar. 1989. Pool at edge of marsh, 2 × 2 m, depth up to 0.7 m, bottom loam, water turbid, beige. *Juncus*, *Chara*, herbaceous plants.

N8928. Small stream in same marsh as N8927, 2 Mar. 1989. Water clear, light brown, flowing through dense marsh vegetation, sample at culvert under road, width 1 m, current c. 10 m/min, depth up to 0.7 m, bottom sand with pebbles.

N8929. Pond at edge of marshy forest. 2 Mar. 1989. *Nymphaea*, *Juncus*.

N8930. Small stream in marsh, 2 Mar. 1989. Open part with flooded banks. Grass-like vegetation along banks with considerable amount of epiphytic algae. Most species from flooded banks, but *Rhagovelia* from the stream.

N8931. C. 15 km S of Pomalaa, 2 Mar. 1989. Sand pits at edge of marsh. Water clear to somewhat turbid, light brown, depth up to 0.5 m.

N8932-N8933: Kecamatan Mowewe.

N8932. Road to Mowewe, 3 Mar. 1989. Narrow stream at edge of marsh, water dark brown, bottom with much muddy detritus and plant debris, some *Azolla*.

N8933. Wide stream near N8932, 3 Mar. 1989. Sample from shallow bay without current, soft loamy bottom, much debris from palmtree leaves.

N8934. Kecamatan Kolaka.

N8934. Road to Kendari, 20 km E of Kolaka, 3 Mar. 1989. Small mountain stream in woodland, 1-1.5 m wide, depth very variable, potholes up to 1 m, current very variable, small waterfalls and ponded sites.

N8935-N8944. Kabupaten Buton

N8935. First stream crossing road from Baubau to the north, 8 Mar. 1989. Downstream of man-made waterfall, width 5 m, depth and current velocity variable, water colourless, somewhat turbid.

N8936. Desa Gareng-gareng, 8 Mar. 1989. Pool with many small fish.

N8937. Desa Gareng-gareng, 8 Mar. 1989. Pool with very few fish.

N8938. Desa Gareng-gareng, 8 Mar. 1989. Dirty pond without fish.

N8939. Road to Lawele, 9 Mar. 1989. Mangrove swamp E of road, bottom with thin layer of mud and mangrove roots, marshy vegetation.

N8940. Lower course of small stream, 9 Mar. 1989. Bottom bare grey sand and mud, some plant debris, sluggish.

N8941. Small mountain stream close to the sea, 9 Mar. 1989. Bottom rocky without sand or pebbles, vary from small waterfalls to nearly stagnant pools, no water vegetation, but banks with dense cover of mosses.

N8942. Road to Parjowiro, about 15 km E of Baubau. 10 Mar. 1989. Small cascade-stream, water turbid, and somewhat milky colour.

N8943. Pool at edge of N8942, 10 Mar. 1989.

N8944. Road to Parjowiro, about 16 km E of Baubau, 10 Mar. 1989. Small stream, anastomosing, ponded sites, marshy forest, many buttressed trees, hilly country.

N8945-N8949. Kabupaten Kendari.

N8945-N8949. Kecamatan Kendari.

N8945. Teluk Kendari, 13 Mar. 1989. Small stream flowing through coconut plantation into bay, bottom sand and clay.

N8946. Teluk Kendari, 13 Mar. 1989. Well near coconut plantation.

N8947. Teluk Kendari, Pulau Bungku Toko, 13 Mar. 1989. Puddles in mangrove.

N8948. Teluk Kendari, close to sea. 13 Mar. 1989. Pool with seawater behind sand wall overgrown with *Ipomoea*.

N8949. Teluk Kendari. 13 Mar. 1989. Well protected by masonry, near N8948.

APPENDIX 2

Localities on Sulawesi and Borneo from recent collections made by J. P. Duffels, J. Huisman, R. de Jong and J. van Tol.

Borneo

14 Mar 1987 – Sabah. 60 km W of Lahad Datu. Danum Valley near Danum Valley Field Centre, brooklet at West 3. Sample B. Alt. 220 m asl. 4°58'N 117°48'E. (J. Huisman).

23 Mar 1987 – Sabah. 60 km W of Lahad Datu. Danum Valley near Danum Valley Field Centre, streamlet near West 11 / North 5. Sample A. Alt. 220 m asl. 4°48'N 117°48'E. (J. Huisman).

3 Apr 1987 – S Sabah. 105 km S of Beaufort: Long Pasia area. Sungai Maga near confluence Sg. Pasia. Alt. 1210 m asl. Larger fast running stream in untouched lower montane evergreen rain forest. Large boulders, rapids. 4°26'N 115°40'E. (J. van Tol).

8-9 Apr 1987 – S Sabah. 105 km S of Beaufort: Long Pasia area. Sungai Ritan. Alt. 1160 m asl. Undisturbed evergreen tropical rain forest. 4°24'N 115°42'E. (J. van Tol & J. Huisman).

- 4 Nov 1987 – Sabah. 20 km W of Sandakan. Sepilok Laut near resthouse. ML light. 5°49'N 118°06'E. (J. Huisman & R. de Jong).
- 23 Nov 1987 – Sabah. 16 km NE Tenom: Agricultural Research Station. Sungai Segalan. At light. 5°12'N 115°59'E. (J. Huisman & R. de Jong).

Sulawesi

- 23 Feb 1985 – Sulawesi Utara. Dumoga-Bone NP. Project Wallace. Edward's Camp. Tumpah river. 900 m asl [recte 600 m]. (J. P. Duffels).
- 15 Mar 1985 – Sulawesi Tengah. Lore Lindu National Park. 10 km NE of Gimpu. Lower montane forest. Rano Rano. Alt. 1600 m asl. Duffels Sta. 42 (J. P. & M. J. Duffels).
- 23 Apr 1985 – Sulawesi Utara. Dumoga-Bone NP. Project Wallace. Waterfall Creek, tributary of Tumpah river. Sample B. c. 225 m asl. UTM WL9768 [recte XL0064]. 0°35'N 123°54'E. (J. van Tol).
- 23 May 1985 – Sulawesi Utara. Dumoga-Bone NP. Project Wallace. Tumpah river near confluence Toraut. Sample A. c. 210 m asl. UTM XL0063. 0°34'N 123°54'E (J. van Tol).
- 3 Jun 1985 – Sulawesi Utara. Dumoga-Bone NP. Project Wallace. Tumpah river near Edward's subcamp. Sample A. Alt. c. 600 m asl. UTM WL9365. 0°35'N 123°51'E. (J. van Tol).
- 4 Jun 1985 – Sulawesi Utara. Dumoga-Bone NP. Project Wallace. Brooklet c. 2 km west of Edward's subcamp. Sample A. c. 700 m asl. UTM WL9269. (J. van Tol).
- 6 Dec 1985 – Sulawesi Tengah. 50 km SE of Palu: Lore Lindu National Park. Sopo valley near Dongi Dongi. Sample B. Alt. 950 m asl. Rainwater puddle without vegetation, near logging road. UTM SJ86. 1°13'S 120°11'E (J. van Tol & J. Krikken).
- 7 Dec 1985 – Sulawesi Tengah. 60 km SE of Palu: Lore Lindu National Park. Danau Taming and brooklets. Sample A. Alt. 1600 m asl. *Pandanus*. 1°20'S 120°15'E. (J. van Tol).
- 8 Dec 1985 – Sulawesi Tengah. 50 km SE of Palu: Lore Lindu National Park. Sopo river near Dongi Dongi. Sample A. Alt. 950 m asl. UTM=SJ86. 1°13'S 120°11'E (J. van Tol).
- 19-21 Oct 1989. – Sulawesi Tengah. SW of Luwuk: Totop camp along Batui river. Alt. 120 m asl. 1°09'S 122°31'30"E. Lowland rainforest. Sample Sul. 18 (J. P. Duffels).
- 20 Oct 1989. – Sulawesi Tengah. Luwuk area. Sungai Tikalalang. Sample 89JvT026. (J. van Tol).

BOOK REVIEW

Medvedev, G. S. (editor-in-chief), 1990. Keys to the Insects of the European Part of the USSR. Volume IV. Lepidoptera, Part 2. – Keys to the fauna of the USSR, 130. English Translation [originally published in Russian, Leningrad, 1981]. – E. J. Brill, Leiden. 1092 pp, 747 figs. [ISBN 90 04 08926 8, price 280 Dutch guilders, ca US \$ 140].

This book is the second volume on Lepidoptera translated into english. The first was published in 1988 and reviewed by the late A. Diakonoff in this journal (vol. 132: 162). While the first volume dealt with the primitive Lepidoptera, the Tortricidae and some primitive Microlepidoptera, this volume treats most of the remaining so-called microlepidopteran families, covering the superfamilies Tineoidea (incl. Gracillariidae and related families, but excluding the Psychidae, which were treated in vol. 1), Yponomeutoidea and Gelechioidea (excluding the Coleophoridae). In total about 1280 species from the European part of the USSR and adjacent countries are covered. Keys are provided up to species level and genitalia of many species are illustrated. Also some adults are illustrated in line-figures.

Although this is a review of the translation, it also presents an opportunity, being unable to read Russian, to review the original contents, bearing in mind that it represents the knowledge of about 1980.

Preparing identification keys for a large order as the Lepidoptera for the huge territory of the European part of the USSR is in itself a large project, which is unprecedented outside the USSR. The keys heavily lean on previously published revisions and keys, mostly published outside the USSR. However, gathering such information is worthwhile, especially for the non-specialist, where the originals are so scattered over journals and books. For some families there is also original input, in particular figures of genitalia of species never illustrated before. Regrettably, many male genitalia have been illustrated in lateral view, where it is now general practice to illustrate male genitalia in taxonomic papers in ventral view, with the valvae spread out. This will make comparison of standard genitalia preparations with the figures difficult, and could lead to misidentifications.

The quality of the various families differs greatly, some are clearly treated by specialists, and contain original information, others are in fact almost copies of foreign literature, like the family Elachistidae, which is merely an abstract of Volume 6 of *Fauna Entomologica Scandinavica* by Traugott-Olsen & Nielsen (now sold by the same publisher as this translation!). Important original treatments are the Gracillariidae by Kuznetsov, the Momphidae and related families by Zagulyaev and Sinev and the Oecophoridae by L'vovskii. The chapter on Gelechiidae by Piskunov is important, because it is the only currently available treatment of European Gelechiidae. Unfortunately, the quality is below expectations, since many species are excluded from the keys, the genitalia illustrations are a collection of copies from other sources, including some very poor ones, and complex original figures in lateral view.

Although it is understandable from the point of costs, what I feel is most missing are colour plates of adult moths. Identification of moths should start with comparison of colour patterns, which is so much easier than to start making preparations of wing venation and genitalia. With this book, identification of an unknown genus is often almost impossible without referring to the genitalia.

I am not able to comment on the quality of the translation, but would like to make two general remarks. Firstly, the reproduction of the figures is poor. Despite the poor quality of paper, the figures in the Russian text are far superior. Secondly, it is to be regretted that the translators have chosen to translate the Russian common host-plant names into common English names. Although there is a list of these names and scientific names at the end of the book, it would have been much easier to include scientific names, where many users will not be familiar with English common plant names.

In conclusion, this translation is an important review of European Microlepidoptera, which temporarily will fill the gap between the older plate books like 'Spuler' and the modern treatments of 'Microlepidoptera Palaearctica', but it should be used with much care, since it is definitely not complete and contains some erroneous information. Those who use the book merely for the illustrations of genitalia, are better off with the original Russian edition, which is also much cheaper.

[E. J. van Nieukerken]

LEAF-MINING LEPIDOPTERA (NEPTICULIDAE, BUCCULATRICIDAE, GRACILLARIIDAE) FROM *ULMUS* IN NORTHERN CASPIYA (KASPIA)

Puplesis, R., Seksjaeva, S. & V. Sruoga, 1991. Leaf-mining Lepidoptera (Nepticulidae, Bucculatricidae, Gracillariidae) from *Ulmus* in northern Caspiya (Kaspiya). – Tijdschrift voor Entomologie 134: 69-73, figs. 1-9. [ISSN 0040-7496]. Published 1 July 1991.

Three leaf-mining species from elm (*Ulmus carpinifolia* Rupp. ex Suckow): *Stigmella kazakhstanica* Puplesis sp. n. (Nepticulidae), *Bucculatrix caspica* Puplesis & Sruoga sp. n. (Bucculatricidae) and *Phyllonorycter schreberella* (F.) (Gracillariidae) are recorded from the northern Caspiyan region (USSR). The new species are described, genitalia and mines are illustrated. *Phyllonorycter schreberella* (F.) is diagnosed and its male genitalia are figured.

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Keywords. – Nepticulidae; Bucculatricidae; Gracillariidae; leaf-mining Lepidoptera; northern Caspiya.

The large northern Caspiyan (=Kaspian) region is generally characterized by a strong continental climate and by arid landscapes. Except oases by the rare rivers and settlements, there are only dry steppes, semideserts and deserts. The abundance of salt lakes, saline soils (solanchaks and solonetzes) is very characteristic. The vegetation of most of these biotopes is extremely poor, usually without woody plants. Grass cover is thin, the vegetation consists mainly of different worms-woods (*Artemisia* spp.) and cereals, with worm-woods dominating. The sum of active temperature equals 2800-3400 °C with a wetting coefficient of 0.15-0.10 (Tushinskij & Davydova 1976).

In oases near the settlements the elm (*Ulmus carpinifolia* Rupp. ex Suckow) is the dominating tree. In a few cases it is the only tree present.

Hardly any published data on leaf-mining Lepidoptera were available from these regions. Only one *Stigmella* (Nepticulidae) specimen deposited in the Zoological institute (Leningrad), reared by G. Lindeman from *Ulmus* sp., from Dzhani-bek (Western Kazakhstan), was known. It belongs to a new species.

During investigations in early August 1988 in the localities (fig. 1) Baskuntschak (Astrakhan Region), Gurjew (Gurjew Region), Beyneu (Mangyschak Region), Kara-Kalpakiya and Kungrad

(Kara-Kalpakskaya ASSR), mines of three leaf-mining Lepidoptera were discovered. *Bucculatrix caspica* Puplesis & Sruoga sp. n. was found in the largest numbers. Numerous cocoons and empty mines were collected from *Ulmus carpinifolia* in all investigated localities, Gurjew and Kungrad. Our later study of 1988 in neighboring Turkmeniya showed its absence from the Central Asiatic part of the USSR. Abundant mines of *Phyllonorycter schreberella* (F.), containing larvae or pupae were collected on *Ulmus carpinifolia* in Baskuntschak. In other places of the Caspiyan region, this species remains yet unrecorded. One empty mine of Nepticulidae was found on *Ulmus carpinifolia* in Baskuntschak, i. e. about 140 km South of Dzhani-bek, where the above mentioned *Stigmella* specimen on *Ulmus* sp. was collected by Lindeman in 1966. It is therefore considered to belong to the same species. *Ulmus* spp. (including *U. carpinifolia* Rupp. ex Suckow) are known to be host plants for Gracillariidae (Kuznetsov 1981), Bucculatricidae (Seksjaeva 1981) and Nepticulidae (Johansson & Nielsen 1990).

No other lepidopterous miners on other plants have been found in this region.

The type specimens are deposited in the collection of the Minological research laboratory at the Department of Zoology of the Pedagogical insti-



Fig. 1. Distribution map of leaf-mining Lepidoptera in northern Caspiya: *Stigmella kazakhstanica* (rectangles), *Bucculatrix caspica* (dots), *Phyllonorycter schreberella* (triangle).

tute, Vilnius, Lithuania (MRL) and in the collection of the Zoological institute of the USSR Academy of Sciences in Leningrad (ZIAS).

TAXONOMIC PART

Nepticulidae

Stigmella kazakhstanica Puplesis sp. n. (figs. 1-3)

Type material. – Holotype ♂: USSR, western Kazakhstan (Kazakh SSR), Dzhanibek, larva on leaf of *Ulmus* sp. (probably *U. carpinifolia*), vi.1966, leg. G. Lindeman (ZIAS). Leaf-mine (no type material): USSR, Astrakhan Region, Baskuntschak, on *Ulmus carpinifolia*, fresh mine, 4.viii.1988, leg. R. Puplesis et V. Sruoga (MRL).

Diagnosis. – Belongs to the *Stigmella ulmivora* group. It is very similar to *S. ulmiphaga* (Preisecker) and *S. ulmivora* (Fologne). In the male genitalia it is easily distinguished by the valvae, which are abruptly broadened at the base. Cornuti not numerous, lateral lobes of vinculum broad in contrast to *S. ulmivora* (Johansson & Nielsen 1990).

Description

Male. – Frontal tuft pale orange. Antennae pale brown. Eye-caps and collar cream. Palpi cream. Thorax and forewings uniform, greyish brown. Cilia and hindwings approximately as forewings in colour.

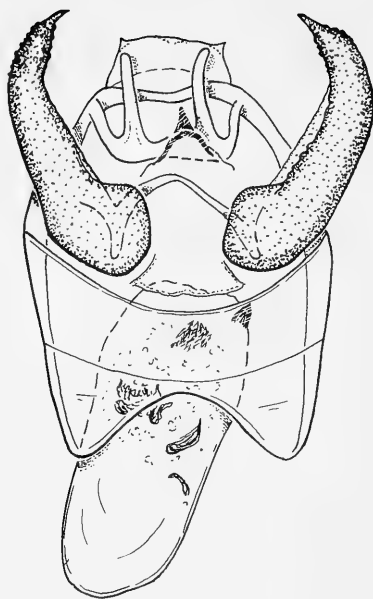


Fig. 2. Male genitalia of *Stigmella kazakhstanica*, holotype (scale 0.1 mm).



Fig. 3. Mine of *Stigmella kazakhstanica* on *Ulmus* sp., from which the holotype was reared.

Female unknown.

Male genitalia (fig. 2). – Valva narrow medially and apically, strongly broadened basally. Transtilla with short sublateral processes. Juxta present, its form resembles a triangle apically. Uncus approximately with trapezium shape, with slightly tapering angles. Gnathos with two thin and long posterior processus. Transverse bar of gnathos narrow. Aedeagus narrowing in middle (in lateral view). Vesica with two groups of cornuti; one of which is larger and situated in middle, a smaller group is situated apically. Cornuti more or less in form of sclerotized spines, some cornuti have different forms.

Biology. – Larvae in June and August, mining leaves of *Ulmus carpinifolia* Rupp. ex Suckow. Mine a contorted gallery (fig. 3). Early mine completely filled with brownish frass; later gradually widening with frass coiled, leaving wide clear margins; finally frass in a dark narrow line.

Distribution (fig. 1). – Only known from the lower Volga valley.

Bucculatricidae

Bucculatrix caspica Puplesis & Sruoga sp. n. (figs. 1, 4-8)

Type material. – Holotype ♂: USSR, Astrakhan Region, Baskuntschak, N 4170, cocoon on leaf *Ulmus carpinifolia*, 4.viii.1988, ex p. 7.viii.1988. Paratypes: 1 ♂, 1 ♀, same data as holotype, ex p. 7-15.viii.1988; 1 ♂, same locality, caught on leaf of *Ulmus carpinifolia*, 4.viii.1988, leg. R. Puplesis and V. Sruoga (MRL). Leaf-mines (no type material): Mangyschlak Region, Beyneu; Kara-Kalpaks-kaya ASSR, Kara-Kalpakiya.

Diagnosis. – This species is similar to the European *B. ulmella* Zeller (Seksjaeva 1981) (on *Quercus*) and the nearctic *B. electa* Braun which also feeds on *Ulmus* leaves (Braun 1963). *B. caspica* is easily recognized by its male genitalia with a long vinculum, the presence of a transtilla and the form of the valvae.

Description

Male (fig. 4). – Forewing length 2.9-3.1 mm. Face creamy white, tuft brown or brownish in central part, with creamy white piliform scales laterally. Eye-caps creamy white. Antennal flagellum with alternating white and brown rings of equal width. Thorax creamy white, slightly mottled, as some scales have brownish tips. Forewing with same colour as thorax, but some brown spots are present. Three or four of these spots are situated on the costal margin, the two below the fold, in apical part of forewing are smaller and usually darker. They include patches of blackish-brown scales. Dark-tipped scales form a line on the pale creamy cilia. Hindwings and cilia greyish cream to pale brownish. Legs cream with little fuscous shading.

Female. – Forewing length about 3.3 mm. Similar to male, but face cream, tuft slightly brownish centrally. The spots on the forewing may be larger than in male.

Male genitalia (fig. 5). – Valva with convex margin medially, suddenly tapering apically. Many large and some short setae on apical and medial part of valva. Transtilla present. Anellus forming an asymmetric ring. Uncus with two large lateral

setosae lobes. Vinculum ventrally a large, more or less triangular lobe, rounded anteriorly. Aedeagus long and slightly bent basally.

Female genitalia (fig. 6). – Apophyses posteriores long. Ductus bursae narrow and very long. Bursa copulatrix more or less oval with numerous small spines.

Egg. – Laid on the underside of a leaf of *Ulmus carpinifolia* Rupp. ex Suckow, generally close to the midrib or a lateral vein. In some cases, eggs are laid away from veins.

Mine (fig. 8). – Gallery very narrow and comparatively long (18-20 mm) with black linear frass, leaving clear margins throughout its whole course.

Cocoon (fig. 7). – Whitish cream with blackish perpendicular patterns.

Distribution (fig. 1). – Probably widespread in northern Caspiya, but possibly absent from the Amudar'ya oases and Turkmeniya.

Gracillariidae

Phyllonorycter schreberella (Fabricius) (fig. 9)

Diagnosis. – It belongs to the *Phyllonorycter ulmifoliella* group, which larvae are usually leaf-miners of *Ulmus* (Kuznetsov 1981). It is easily recognized from all other species in that group by the silvery shining frons, thorax and base of the forewings. Tuft on head black. Forewing with two silver fasciae basally and medially, two silver spots apically. There is a black spot on base of forewing, near costal margin. Male genitalia (fig. 9) differs from all other species of the genus by the narrow and bent valvae.

Distribution (fig. 1). – *P. schreberella* is found in Europe from England and Scandinavia to the Balkans and the European part of the USSR, also in Asia Minor, the Caucasus and the mountains of Turkmeniya (Kopet-Dag ridge) (Kuznetsov 1981). The species is here recorded for the first time from the northern Caspiyan region.

Material examined. – 2 ♂, 1 ♀, USSR, Astrakhan region, Baskuntschak, mines 4.viii.1988, ex p. 7.viii.1988, leg. R. Puplesis and V. Sruoga (MRL).

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We thank Zigmantas Gudzinškas (Vilnius) for the identification of *Ulmus carpinifolia*.

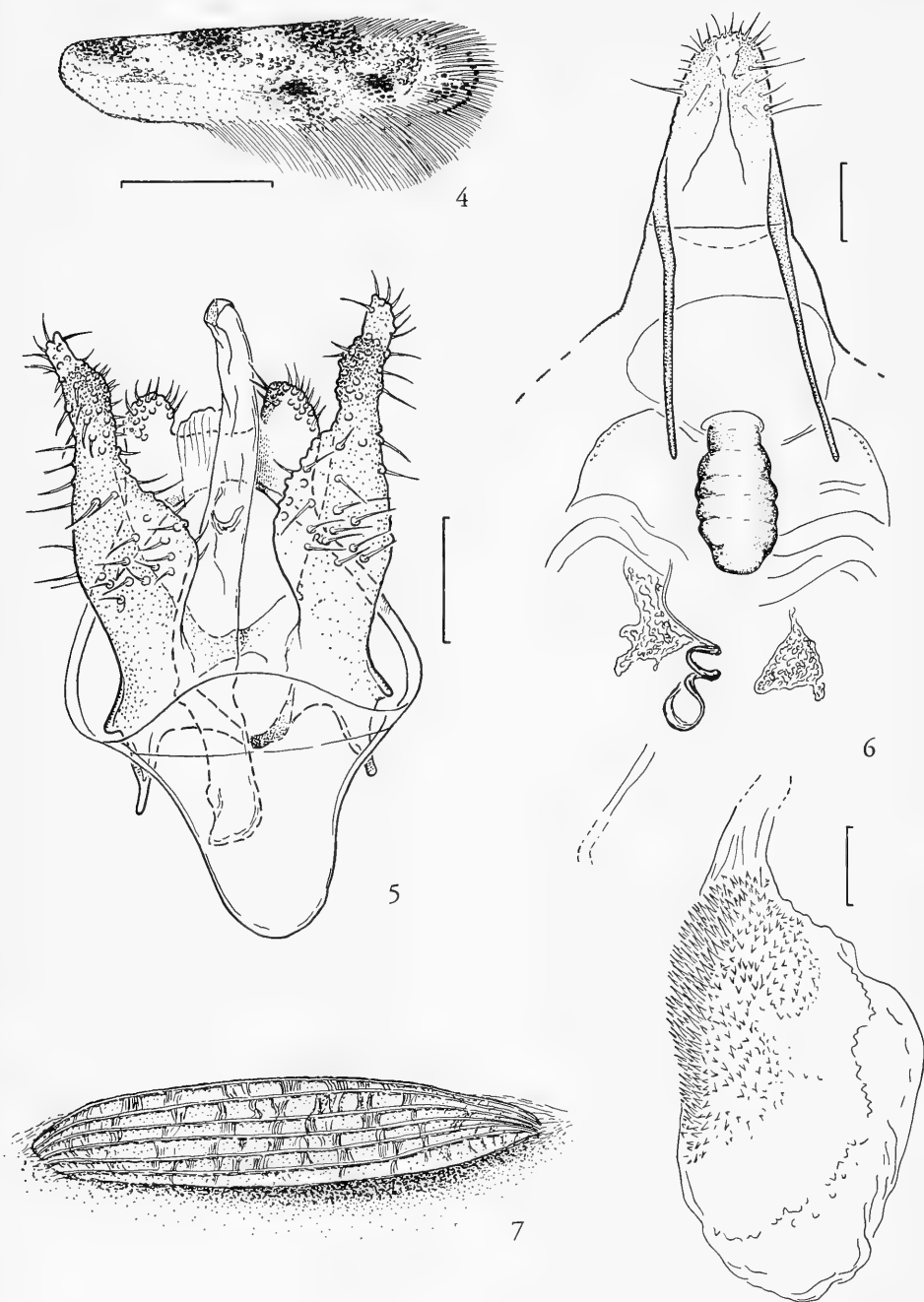


Fig. 4-7. *Bucculatrix caspica*. – 4, forewing (scale 1 mm); 5, male genitalia, holotype (scale 0.1 mm); 6, female genitalia, paratype (scale 0.1 mm); 7, cocoon, from type locality.

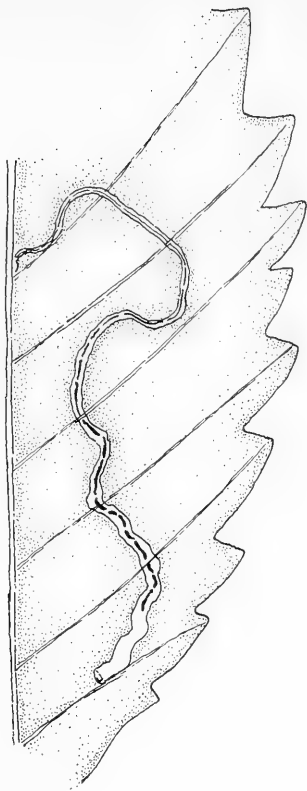


Fig. 8. Mine of *Bucculatrix caspica* on *Ulmus carpinifolia*.

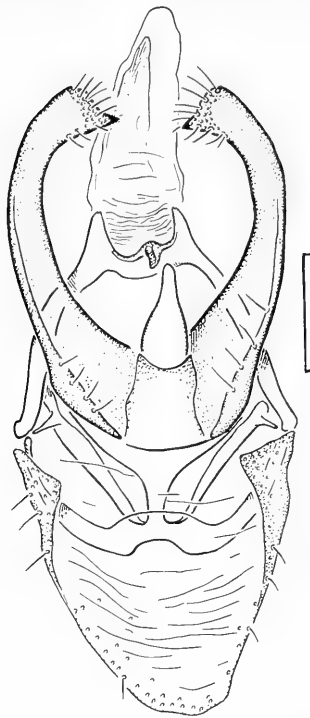


Fig. 9. Male genitalia of *Phyllonorycter schreberella* (F.) (scale 0.1 mm).

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BOOK REVIEWS

Emmet, A. M., 1991. The scientific names of the British Lepidoptera. Their history and meaning. – Harley Books, Colchester, England. 288 pp., viii plates. [ISBN 0 946589 35 6, paperback edition. Price ca US \$ 40].

Many entomologists consider scientific names simply as labels of the subjects of their studies, and do not bother about their meaning. Others, however, are interested in the history of the name and wonder why they are named as they are. To cite the author of this book: 'There is no need to seek the explanations of scientific names, just as there is no need to do crossword puzzles. There are, however, many who derive pleasure from both pursuits.'

For those who are interested in the history of names in general and nomenclature of Lepidoptera in particular, Colonel Emmet has provided a wealth of interesting information, with explanations of names of all British species, genera and families, including a few synonyms, 3000 names in total. The author not only tried to give the exact meaning of the latin or greek words from which the name supposedly was derived, but also tried to trace the reasons of the author for giving it this particular name. This was no small task, when one realises that very few authors before this century ever explained the new names they were proposing. In many cases therefore Emmet had to guess at the thoughts of the name-giving authors, but was greatly helped by his immense knowledge of British Lepidoptera. The systematic section of this book therefore, is by no means a dry dictionary, but well readable and full of small interesting stories about authors of the past. Emmet also could rectify many earlier explanations, by his combined knowledge of the classic languages and Lepidoptera.

That with so many names a few misinterpretations or errors were noted, is a very minor flaw indeed. To cite some, noted by the reviewer: 34. *Ectoedemia occultella*. It is very unlikely that Linnaeus was indicating the larval habits of this species: he described it from specimens which he found on his window. The genus *Trifurcula* (page 45) was named after the three-forked radius in the hindwing, not forewing. Caradja (species 871a) was a Rumanian entomologist, not German.

The introduction is a well written history of nomenclature in Lepidoptera, and gives insight in the way early authors, like Linnaeus, formed scientific names. It also explains the curious usage of special endings for particular groups of Lepidoptera (such as -ella, -ana, -ata). Emmet follows,

against his classical background, the current lepidopterological practice to use original spellings and endings, without bothering about gender of the generic name.

Colonel Emmet has written an invaluable source of information and fun. The book is warmly recommended to all entomologists interested in names, and should not be missing in the library of any lepidopterist.

[E. J. van Nieuwerkerken]

Rubtsov, I. A., 1990. Blackflies (Simuliidae). – Fauna of the USSR, Diptera, Volume 6, Part 6: p. i-xxviii + 1-1042, figs. 1-424 [mostly composite]. [ISBN 90 04 088717, distributed outside India by E. J. Brill, Leiden. Price 300 Dutch Guilders, appr. US \$ 150].

According to information provided by the publishers 'the purpose of the present volume is to provide brief descriptions of species and new identification keys. It primarily incorporates numerous additions to the first addition of the Fauna of the USSR. This second edition also includes 18 species from countries adjoining the Palearctic region, which have not been recorded to-date in the Soviet Union, and 30 species described by Enderlein from Europe (whose description has been improved upon), which may be discovered later in the Soviet Union'.

Usually translations of Russian handbooks are most welcome, but one may doubt whether this is also true in this particular case. Firstly the original was published as early as 1956. Secondly, the text is clearly out of date, since a revised and more comprehensive work by the same author appeared between 1959 and 1964 in Lindner's 'Die Fliegen der palaarktischen Region' in the German language. Thus, for scientists who understand German the information was already available for more than 25 years. I suppose that most dipterists not fluent in German or Russian would have preferred a translation of Lindner rather than one of the Fauna of the USSR. The translation as such seems to be done with reasonable care. For instance, the translator notifies the reader about possible mistakes in the original text, and there is also a translation of the lettering in the illustrations. As usual the quality of the Indian printing is far behind European standards, making some figures difficult to understand. Comparing the three works it appears that the figures in Lindner are by far the best. [J. van Tol]

REVISION OF THE PALAEARCTIC SPECIES OF *HALIPLUS* SUBGENUS *LIAPHLUS* GUIGNOT (COLEOPTERA: HALIPLIDAE)

Vondel, B. J. van, 1991. Revision of the palaearctic species of *Haliplus* subgenus *Liaphlus* Guignot (Coleoptera: Haliplidae). – Tijdschrift voor Entomologie 134: 75-144, figs. 1-312. [ISSN 0040-7496]. Published 1 July 1991.

The palaearctic species of the subgenus *Liaphlus* Guignot, genus *Haliplus* Latreille, are revised. Thirty species are recognised. The following new synonyms are established: *H. modestus* Zimmermann as a junior synonym of *H. eximis* Clark, *H. subguttatus* Crotch and *H. salinarius* Wallis of *H. fulvus* (Fabricius), *H. pelopis* Sahlberg of *H. guttatus* Aubé, *H. syriacus* Wehncke and *H. zimmermanni* Gschwendtner of *H. maculatus* Motschulsky and *H. transvolgensis* Semenov of *H. variegatus* Sturm. Eight new species are described: *H. angusi*, *H. astrakhanus*, *H. davidi*, *H. excoffieri*, *H. gafnyi*, *H. holmeni*, *H. jaechi* and *H. ortalii*. A key to the species is provided. Most primary types have been examined. Lectotypes have been designated for *H. abbreviatus* Wehncke, *H. andalusicus* Wehncke, *H. basinotatus* Zimmermann, *H. dalmatinus* Müller, *H. dalmatinus* var. *weberi* Müller, *H. interpunctatus* (Marsham), *H. lapponum* Thomson, *H. fulvus sparreschneideri* Munster, *H. guttatus* Aubé, *H. maculatus* Motschulsky, *H. pelopis* Sahlberg, *H. cinereus* Aubé, *H. ovalis* Sharp, *H. sharpi* Wehncke, *H. syriacus* Wehncke, *H. zimmermanni* Gschwendtner, *H. variegatus* ab. *pallidior* Müller, *H. leopardinus* Sahlberg and *H. transvolgensis* Semenov.

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Key words. – *Liaphlus*, palaearctic region, China, new species.

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INTRODUCTION

This revision deals with the palaearctic species of *Liaphlus*, a subgenus of *Haliplus*, one of the five genera of the waterbeetle-family Haliplidae. The latest revision of *Haliplus* in the palaearctic region was by Zimmermann (1924). The status of some species remained uncertain. Afterwards some new

species have been described from the southern and eastern parts of the region. Various problems in recognizing and identifying species make a revision necessary.

In 1928 Guignot erected the subgenus *Liaphlus* for the *Haliplus*-species lacking the pronotal basal plicae and possessing a setiferous striae on the dorsal side of the metatibia. Afterwards Guignot (1955) proposed a division of *Liaphlus* into 9 species-groups, of which 4 groups are represented in the palaearctic region as treated in this revision. Especially outside the palaearctic region his division is certainly in some cases based upon misinterpretations. For instance the oriental species *Haliplus angustifrons* Régimbart and *H. arrowi* Guignot are placed in different groups. In my opinion however, these species are very closely related. A similar case is *Haliplus pulchellus* Clark and *H. diopus* Guignot, also placed in different groups, but also closely related.

The subgeneric status of *Haliplus laminatus* (Schaller) is not completely clear. According to the

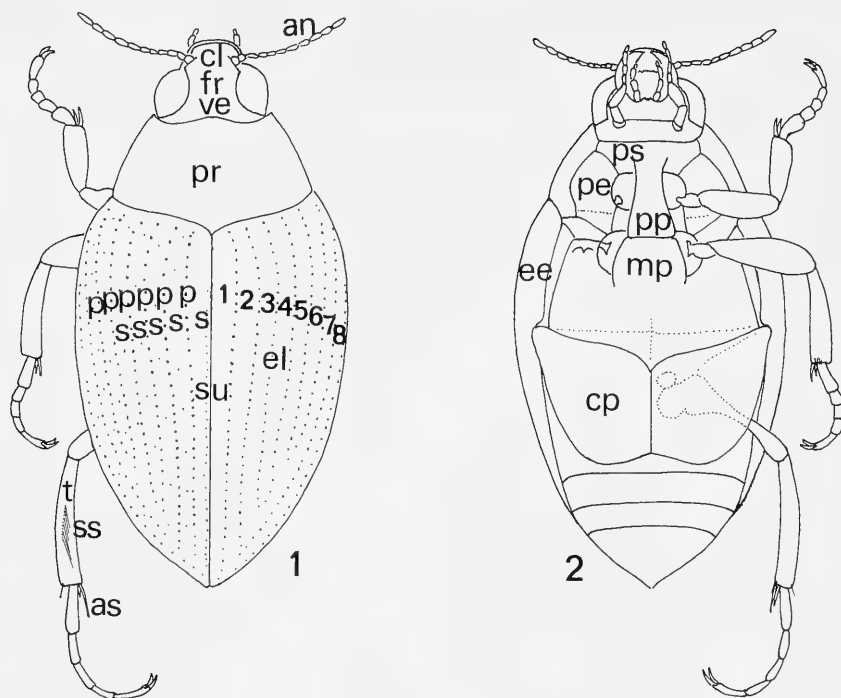


Fig. 1. *Haliplus flavicollis*, dorsal view. – an, antenna; as, apical spur; cl, clypeus; el, elytron; fr, frons; 1, 2, 3, etc, first, second, third, etc. elytral interval; p, primary puncture-row; pr, pronotum; s, secondary puncture-row; su, suture; ss, setiferous striole; t, tibia; ve, vertex.

Fig. 2. *Haliplus flavicollis*, ventral view. – cp, hind coxal plate; ee, elytral epipleuron; mp, metasternal process; pe, proepisternum; pp, prosternal process; ps, prosternum.

definitions for *Liaphlus* it should belong to that subgenus, but the larval stages are distinctly different and very much like the larvae found in the subgenus *Haliplus* s. str. (sensu Guignot 1928) (Vondel 1986).

Beutel & Ruhna (1990) made a phylogenetic analysis of the genera of Haliplidae based on characters of adults. However, on subgeneric level and below much more study is needed to elucidate the phylogenetic relationships within the Haliplidae. For that reason I refrain from dividing the species in this revision into species-groups. They are simply treated in alphabetical order.

For many species the type-material was studied. For some species, of which the status seemed clear to me, only few or no attempts have been made to trace and study the type-material. In some other cases several attempts to locate the types failed. About 2800 specimens have been studied, mostly from Western Europe. Eastern and Southern palaearctic material is relatively scarce in the collections I had access to.

For all species (re)descriptions are provided.

Female genitalia are not described, because they usually are very uniform and further research is necessary to check if there are characters reliable enough to separate related species.

Descriptions of larvae are not included.

METHODS

Before dissecting the aedeagus the beetles are softened in water with detergent for about 2 hours. The aedeagus is pulled out with a small hooked needle and placed into a drop of alcohol. During dissection the beetle has to be kept wet, to prevent the severed aedeagus jumping out of sight. In alcohol the left- and right parameres are separated from the penis by using fine needles. When the alcohol has almost dried up the three parts are usually glued with Fauré-mixture on the same piece of cardboard as the beetle. The penis and the parameres are positioned so that they are seen from

the side. The water-soluble Fauré-mixture makes it possible to loosen the genitalia to study them in an other position or to make temporary slide mounts. In some cases the genitalia are transferred into Euparal on a plastic card, covered by a coverslip and pinned to the original needle. Genitalia should not be glued to plastic cards with water-soluble glue as they are liable to become detached in time.

Drawings of genitalia are made by using a Swift universal microscope with a camera lucida attachment. The other drawings are made by using a Zeiss binocular with an ocular-micrometer.

Measurements are made by using the ocular-micrometer of a Zeiss binocular.

Morphological terms are according to figs. 1 and 2.

The palaearctic region as treated in this revision comprises Europe including Iceland, North Africa north of the Sahara and Asia north of the line formed by the northern borders of Pakistan, India, Nepal, Bhutan, Burma, Laos and Vietnam. For practical reasons Taiwan and China as a whole are taken into account, although the south-eastern part has an oriental fauna.

Material of many institutions and private persons has been studied, including a number of primary types. Locality-names are given, as far as possible, according to the Times Atlas of the World (Comprehensive edition, 1983). Deviating names on original labels are cited, when necessary, in parentheses. In a number of cases I was not able to trace the locality, because of the poor or unreadable labels. Countries are used with their present-day boundaries.

Distribution-maps are based on material examined. Reliable literature-records are included, but using different symbols.

Data on biology are seldom present on labels, so notes on the biology are mainly based on literature and the author's experience. If nothing is mentioned in the descriptions about biology, such information was unknown to the author.

The institutions from which material has been examined or which are otherwise referred to in the text have been abbreviated according to Arnett & Samuelson (1986) with the addition of:

HUJI – IES Laboratory, Hebrew University of Jerusalem, Israel.

MSNT – Museo Civico di Storia Naturale, Trieste, Italy.

MOG – Museum voor het Onderwijs Museon, 's Gravenhage, Netherlands.

RIN – Rijks Instituut voor Natuurbeheer, Leersum, Netherlands.

Further material from the following private collections has been studied: Angus, Englefield Green,

UK; van Berge Henegouwen, Zoetermeer, Netherlands; Cuppen, Ede, Netherlands; Drost, Wadenhoijen, Netherlands; Giessen, Gaanderen, Netherlands; Hielkema, Gouda, Netherlands; Huijbregts, Leidschendam, Netherlands; Jongema, Wageningen, Netherlands; Kanaar, Leiderdorp, Netherlands; Leblanc, Troyes, France; Matsui, Hondo City, Japan; Onder de Linden, Krimpen aan de IJssel, Netherlands; Rotzer, Gampel, Switzerland; Schilthuisen, Leiden, Netherlands; Schreijer, Alkmaar, Netherlands; Sung Hwa Lee, Taegu, Korea; Vallenduuk, Lelystad, Netherlands; Vondel, Hendrik Ido Ambacht, Netherlands.

SYSTEMATIC SECTION

Subgenus *Liaphlus* Guignot

Haliplus sg. *Liaphlus* Guignot, 1928: 138. Type species: *Dytiscus fulvus* Fabricius, 1801, by subsequent designation (Guignot 1930: 75).

Haliplus sg. *Hoplites* Kinel, 1929: 219. Preoccupied. [See remarks under *Haliplus laminatus*.] Type species: *Dytiscus laminatus* Schaller, 1783, by monotypy.

Liaphlus Guignot; Guignot 1933: 228, 1947: 48, 1959: 33, Balfour-Browne 1936: 76, 1938: 12, Csiki 1946: 558, Zaitsev 1953: 43, Freude 1971: 15, Galewski 1976: 27, Franciscolo 1979: 108, Vondel 1986: 132, Holmen 1987: 110, Beutel & Ruhna 1990: 11.

Diagnosis. – The following character set is diagnostic for specimens of this subgenus:

1. Pronotum without basal plicae.
2. Metatibia with a setiferous striole on dorsal face.
3. Males: right paramere with a solid digitus. This is not the case in *H. laminatus* (see remarks under that species).

Remarks. – *Liaphlus* is represented in all faunal regions. Beutel & Ruhna (1990) examined a large number of characters of nine species of *Liaphlus* from different faunal regions, but they did not find evidence for the monophyly of the subgenus.

Within the Haliplidae *Liaphlus* can be recognised by means of the following keys.

Key to the genera of world Haliplidae

1. Last segment of palpi longer than penultimate segment. Metacoxal plates at least covering part of sixth abdominal sternite.....
..... *Peltodytes* Régimbart
- Last segment of palpi clearly shorter than penultimate segment. Last three abdominal sternites freely visible.....2

2. Head as wide as pronotum. Elytra strongly punctured, not in rows..... *Algophilus* Zimmermann
- Head not as wide as pronotum. Elytra with clear rows of punctures..... 3
3. Pronotum almost square, front-corners strongly rounded, elytra usually with longitudinal ridges..... *Brychius* Thomson
- Pronotum widest at base, sides converging anteriorly, elytra without longitudinal ridges in first six intervals..... 4
4. Median part of prosternum and base of prosternal process forming a plateau-like elevation, at least in part angularly separated from sides of prosternum..... *Haliplus* Latreille
- Prosternum evenly rounded from side to side..... *Apteraliplus* Chandler

Note: *Algophilus* is restricted to South Africa, while *Apteraliplus* is only known from North America.

Key to the palaearctic subgenera of *Haliplus*:

1. Dorsal and ventral side of body with clearly visible (30 x) micropunctuation, on elytra between small primary punctures..... *Haliplidius* Guignot
- Elytra smooth or with much weaker micropunctuation (visible at 50 x) between strong primary puncture-rows..... 2
2. Hind tibia with a setiferous striole on dorsal face. Pronotum without basal longitudinal plicae..... *Liaphlus* Guignot
- Hind tibia without a setiferous striole on dorsal face. Base of pronotum on both sides with a, sometimes very short, rarely absent, longitudinal plica..... 3
3. Pronotal plicae reaching beyond middle and strongly bent..... *Neohaliplus* Netolitzky
- Pronotal plicae not reaching beyond middle, straight or slightly curved.... *Haliplus* s.str.

Checklist of palaearctic *Haliplus* (*Liaphlus*)

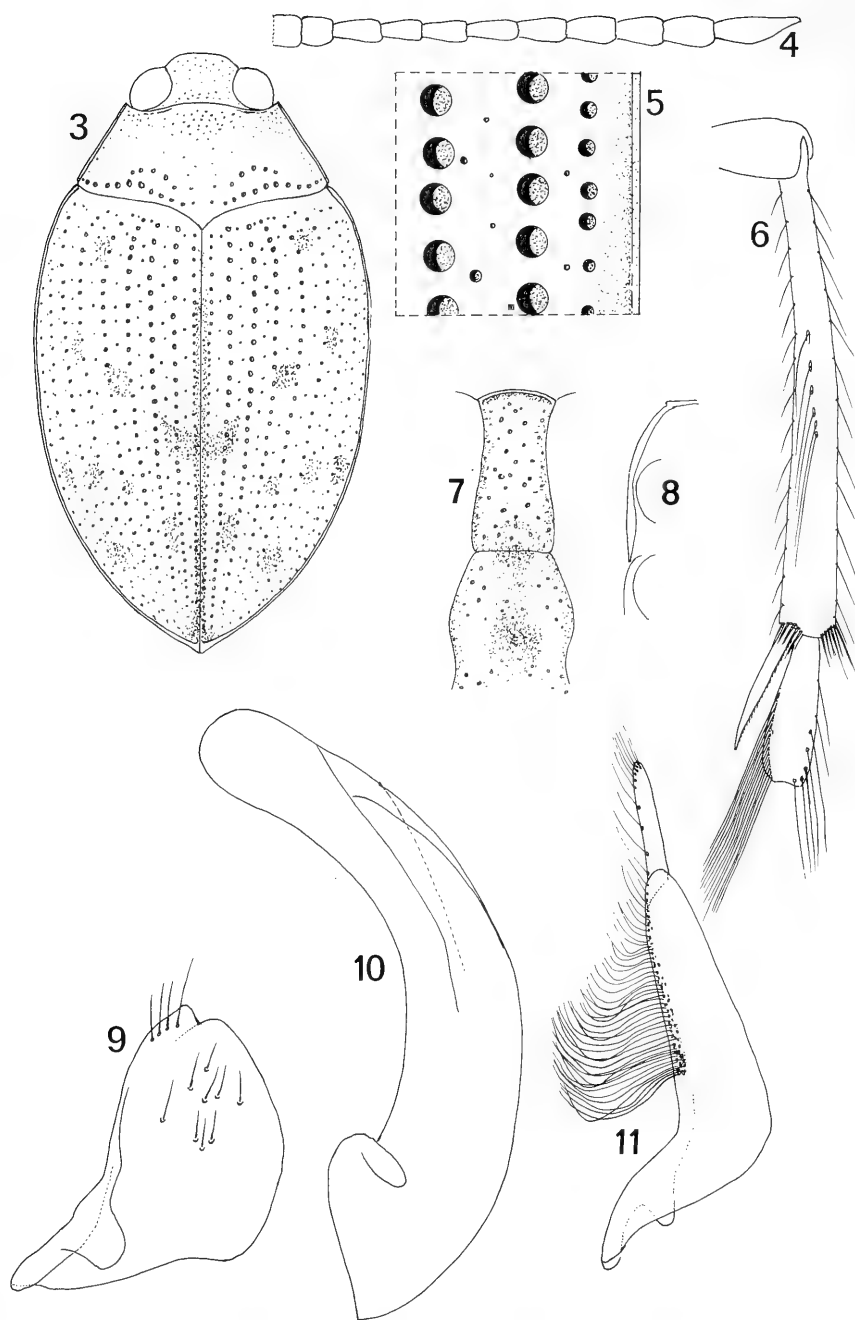
1. *H. abbreviatus* Wehncke, 1880
2. *H. andalusicus* Wehncke, 1874
3. *H. angusi* sp. n.
4. *H. astrakhanus* sp. n.
5. *H. basinotatus* Zimmermann, 1924
6. *H. chinensis* Falkenström, 1932
7. *H. dalmatinus* J. Müller, 1900
8. *H. davidi* sp. n.
9. *H. diruptus* Balfour-Browne, 1946
10. *H. excoffieri* sp. n.

11. *H. eximis* Clark, 1863
H. modestus Zimmermann, 1924 syn. n.
12. *H. flavicollis* Sturm, 1834
13. *H. fulvus* (Fabricius), 1801
H. subguttatus Crotch, 1873 syn. n.
H. salinarius Wallis, 1933 syn. n.
14. *H. gafnyi* sp. n.
15. *H. guttatus* Aubé, 1836
H. pelopis Sahlberg, 1907 syn. n.
16. *H. holmeni* sp. n.
17. *H. jaechi* sp. n.
18. *H. kotoshonis* Kano & Kamiya, 1931
19. *H. kulleri* Vondel, 1988
20. *H. laminatus* (Schaller, 1783)
21. *H. maculatus* Motschulsky, 1860
H. syriacus Wehncke, 1880 syn. n.
H. zimmermanni Gschwendtner, 1921 syn. n.
22. *H. maculipennis* Schaum, 1864
23. *H. mucronatus* Stephens, 1828
24. *H. ortalii* sp. n.
25. *H. ovalis* Sharp, 1884
26. *H. pulchellus* Clark, 1863
27. *H. rubidus* Perris, 1857
28. *H. sharpi* Wehncke, 1880
29. *H. variegatus* Sturm, 1834
H. transvolgensis Semenov, 1904 syn. n.
30. *H. villiersi* Legros, 1972

Key to the palaearctic species of *Liaphlus*

1. Distance between eyes about eye-width (fig. 170, 208, 244)..... 2
- Distance between eyes at least 1.2 × eye-width..... 4
2. Prosternal process furrowed on both sides (fig. 248)..... 26. *pulchellus*
- Prosternal process strongly impressed in middle, at least in apical half (fig. 174)..... 3
3. Elytra with basal black band, eighth puncture-row with about nine small dark blotches..... 22. *maculipennis*
- Elytra without basal black band, eighth puncture-row not with dense row of dark blotches..... 18. *kotoshonis*
4. Head relatively wide (fig. 217), distance between eyes at least 2.3 × eye-width. Metasternal process flat in middle. Elytra without dark blotches..... 23. *mucronatus*
- Head narrower. Metasternal process at least with small pit or groove in middle..... 5
5. Sides of prosternal process before coxae extending forwards as complete plicae to anterior edge of prosternum (fig. 8)..... 8
- Sides of prosternal process before coxae not completely extending forwards as plicae to an-

- terior edge of prosternum (fig. 116).....6
6. Plicae on sides of prosternal process widely interrupted before coxae (fig. 17). Longer apical spur of hind tibia usually as long as or longer than first tarsal segment (fig. 15). Elytra mostly with darker blotches.....*2.andalusicus*
- Plicae on sides of prosternal process completely absent before coxae (fig. 116). Elytra without clear blotches. Apical spurs of hind tibia not as long as first tarsal segment.....7
7. Punctures of primary elytral rows wide in basal area, distance between rows not more than diameter of punctures (fig. 255). Distance between eyes $1.7-1.9 \times$ eye-width.....*27.rubidus*
- Punctures of primary elytral rows rather small, distance between rows more than diameter of punctures (fig. 113). Distance between eyes $1.4-1.6 \times$ eye-width.....*12.flavicollis*
8. Setiferous striole on dorsal face of hind tibia stretched over apical half (fig. 195). Elytra usually with more or less confluent and interrupted dark lines following rows of dark punctures, but distinct blotches usually absent. Basal elytral punctures coalescing to form short grooves (fig. 188). Male: first tarsal segment of midlegs strongly dilated ventrally (fig. 192). Female: elytra almost completely covered with micro-punctures.....*20.laminatus*
- Setiferous striole on dorsal face of hind tibia usually not longer than $\frac{1}{2} \times$ tibia length, not reaching apical point. Male: first 3 tarsal segments of midlegs weakly dilated ventrally. Female: elytra without clear micropunctuation.....9
9. Elytra without dark blotches. Pronotal and elytral punctures black.....*11.eximis*
- Elytra with dark blotches, or when these blotches are strongly reduced or absent punctures on disc of pronotum are not black10
10. Elytra with basal transverse black band as dark as sutural maculation.....*34*
- Elytra without basal black band. Sometimes some transverse darkening separated from basal margin or a brown basal band, clearly less dark than sutural maculation.....11
11. Widened basal punctures on pronotum twice the width of elytral primary punctures (fig. 141). Body-shape parallel or subparallel. Prosternal process narrow, length $2.6 \times$ width, slightly narrowed near coxae (fig. 145). Elytra with mostly vague blotches, one large blotch on middle of suture and three smaller ones on each elytron.....*15.guttatus*
- Basal punctures on pronotum usually not twice as wide as elytral primary punctures. Body not clearly parallel.....12
12. Length 3.6-4.5 mm.....29
- Length 2.6-3.6 mm.....13
13. Elytra with longitudinal distinct blotches in even intervals, blotches not connected to darkened suture.....14
- Elytral blotches different.....17
14. Metasternal process flat anteriorly. Vertex darkened.....15
- Metasternal process grooved anteriorly. Vertex not darkened16
15. Setiferous striole weak, about $\frac{1}{6} \times$ tibia length (fig. 33). First elytral primary puncture-row with about 28 punctures. Pronotum anteriorly partly bordered. Males: left paramere with solid digitus (fig. 36).....*4.astrakhanus*
- Setiferous striole strong, about $\frac{1}{3} \times$ tibia length (fig. 202). First elytral primary puncture-row usually with more than 28 punctures. Pronotum anteriorly not bordered. Males: left paramere without solid digitus.....specimens of *21.maculatus*
16. Distance between eyes less than $1.7 \times$ eye-width. Males: top of penis short (fig. 64).....specimens of *7.dalmatinus*
- Distance between eyes more than $1.7 \times$ eye-width. Males: top of penis long, usually slightly widened apically (fig. 278).....specimens of *29.variegatus*
17. Elytra with large maculation, discal blotch and blotch in apical part connected to darkened suture.....18
- Elytra with usually vague maculation on first and even intervals, or only darkening on discal parts of puncture-rows, blotches on apical part not connected to suture.....21
18. Length of prosternal process $2.6 \times$ width (fig. 25).....*3.angusi*
- Length of prosternal process less than $2.4 \times$ width.....19
19. Prosternal process hardly narrowed near coxae (fig. 73). Males: left paramere with short digitus.....*8.davidi*
- Prosternal process clearly narrowed near coxae. Males: left paramere without digitus.....20
20. Distance between eyes more than $1.7 \times$ eye-width.....specimens of *29.variegatus*
- Distance between eyes less than $1.7 \times$ eye-width.....specimens of *9.diruptus*
21. Metasternal process grooved anteriorly, weakly punctured.....22
- Metasternal process flat anteriorly.....23
22. Prosternal process impressed posteriorly (fig. 287). Elytral primary puncture-rows sparse, sutural punctures weak (fig. 285).....*30.villiersi*
- Prosternal process posteriorly at most with weak transverse impression (fig. 7). Elytral primary puncture-rows dense, sutural punctures strong (fig. 5).....*1.abbreviatus*



Figs. 3-11. *Haliplus abbreviatus*, locality unknown. - 3, dorsal view; 4, antenna; 5, elytral punctuation; 6, dorsal side of hind tibia; 7, prosternal process; 8, lateral view of prosternal process; 9, left paramere; 10, penis; 11, right paramere.

23. Males.....24
 - Females.....27
24. Left paramere without solid digitus 14.*gafnyi*
 - Left paramere with solid digitus.....25
25. Digitus on left paramere long and parallel-sided. Base of pronotum with about five stronger punctures on both sides.... 19.*kulleri*
 - Digitus on left paramere tapering. Base of pronotum with almost continuous row of stronger punctures.....26
26. Left paramere with strongly developed tapering digitus, row of long hairs on inner margin of paramere.....17.*jaechi*
 - Left paramere with small tapering digitus, at most some short hairs on inner margin of paramere.....24.*ortali*
27. Metasternal process flat with shallow pit in middle, strongly and densely punctured, small punctures between large ones (fig. 136)..... 14.*gafnyi*
 - Metasternal process with clear pit in middle, sparsely and moderately strongly punctured (fig. 183)..... 28
28. Basal punctures on pronotum weak and reduced in the middle (fig. 179). Prosternal process weakly narrowed (fig. 183)..... 19.*kulleri*
 - Base of pronotum with continuous row of strong punctures (fig. 161). Prosternal process strongly narrowed (fig. 165)..... 17.*jaechi* or 24.*ortali*
29. Distance between eyes less than $1.4 \times$ eye-width.....30
 - Distance between eyes more than $1.4 \times$ eye-width.....31
30. Black suture not reaching first secondary puncture-row in basal part (fig. 91). Body strongly tapering apically. Penis and parameres figs. 99-101.....10.*excoffieri*
 - Black suture reaching first secondary puncture-row in basal part (fig. 48). Body more oval. Penis and parameres figs. 54-56.....6.*chinensis*
31. Elytral discal blotch connected to suture. Penis and parameres figs. 241-243.....25.*ovalis*
 - Elytral discal blotch not connected to suture.....32
32. Length of hind tarsus including claws more than $1.3 \times$ tibia length. Prosternal process slightly narrowed near coxae, narrowed part 0.6 to $0.7 \times$ widest part. Punctures of setiferous striole not connected in a groove. Male: digitus of right paramere $\frac{1}{5} \times$ length of basal part.... large specimens of 7.*dalmatinus*
 - Length of hind tarsus less than $1.3 \times$ tibia length. Prosternal process strongly narrowed near coxae, narrowed part $0.5 \times$ width of widest part.....33
33. Distance between eyes less than $1.6 \times$ eye-width. Setiferous striole on dorsal side of hind tibia not strongly grooved, separate points usually clearly visible. Male: apical part of penis very narrow and pointed (fig. 205).....21.*maculatus*
 - Distance between eyes more than $1.6 \times$ eye-width. Setiferous striole on dorsal side of hind tibia strongly grooved, separate points not or hardly visible. Male: apical part of penis wide and rounded at the top (fig. 127).....13.*fulvus*
34. Length 3.5-4.1 mm. Black sutural stripe in anterior half at most reaching first secondary puncture-row.....5.*basinotatus*
 - Length at most 3.6 mm. Black sutural stripe reaching first primary puncture-row.....35
35. Distance between eyes about $1.2 \times$ eye-width. Prosternal process wide, impressed apically, weakly narrowed near coxae (fig. 155). Setiferous striole on dorsal side of hind tibia consisting of about 6 isolated points, not grooved (fig. 154). Male: left paramere with solid digitus (fig. 158). Between fore-claws a small cushion (fig. 153).....16.*bolmeni*
 - Distance between eyes 1.3 - $1.5 \times$ eye-width 36
36. Fourth and fifth antennal segment about as long as wide (fig. 263). Punctures in first to fourth primary elytral rows weaker than in other puncture-rows. Prosternal process broad, hardly narrowed near coxae, hardly or not impressed apically (fig. 266). Anterior edge of prosternum clearly and completely bordered.....28.*sharpi*
 - Fifth antennal segment clearly longer than wide. Inner primary puncture-rows of elytra not weaker than outer ones. Prosternal process strongly narrowed near coxae, strongly impressed apically. Anterior edge of prosternum only bordered near process. South-east palaeartic or north oriental specimens of.....9.*diruptus*

DESCRIPTION OF THE PALAEARTIC SPECIES OF LIAPHLUS

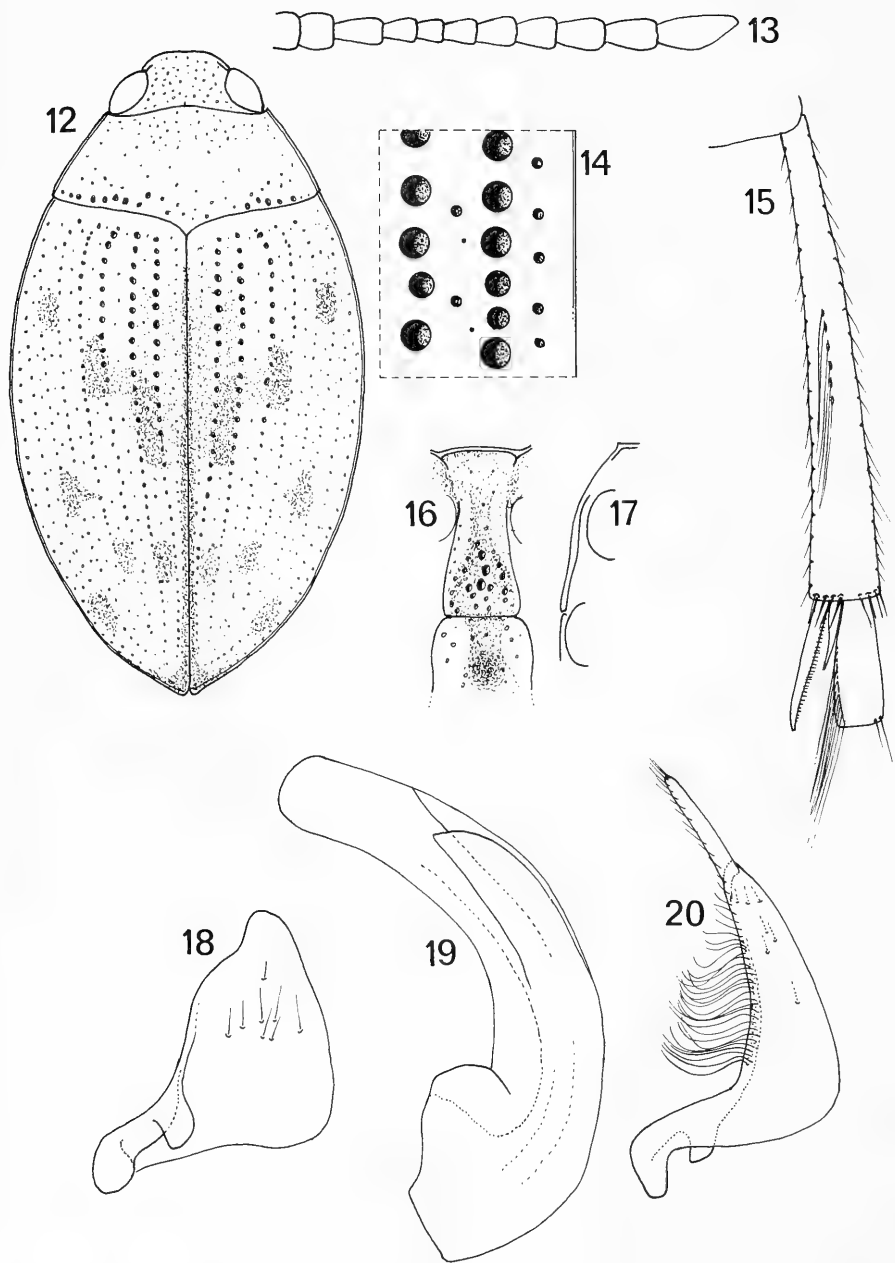
1. *Haliplus abbreviatus* Wehncke (figs. 3-11)

Haliplus abbreviatus Wehncke, 1880: 73. Lectotype ♀ (here designated), [Iraq] 'Mesopotamia, Sharp' (MNHN) [examined].

Haliplus abbreviatus; Zimmermann 1920: 303, 1924: 136, Alfieri 1976: 38.

Diagnosis

This species is closely related to *villiersi* or even conspecific. Specimens of *villiersi* have the prosternal process more impressed posteriorly, the prim-



Figs. 12-20. *Haliplus andalusicus*, lectotype. – 12, dorsal view; 13, antenna; 14, elytral punctuation; 15, dorsal side of hind tibia; 16, prosternal process; 17, lateral view of prosternal process; 18, left paramere; 19, penis; 20, right paramere.

ary elytral puncture-rows sparser and the sutural punctures weaker.

Description

Length 3.0 mm, width 1.7 mm. Body oval, widest in the middle (fig. 3).

Head. – Light brown, rather strongly punctured, more sparsely punctured between the eyes (fig. 3). Distance between the eyes $1.6 \times$ eye-width. Antennae (fig. 4) and palpi yellow-brown.

Pronotum. – Yellow-brown, base and front margin slightly darkened. Lateral borders straight to slightly convex, with fine dark margins. Disc sparsely punctured, front margin behind an unpunctured zone with a strongly punctured band, base strongly punctured, basal puncture-row partly widened and darkened (fig. 3).

Elytra. – Yellow-brown with in the anterior half fairly strong and apically weaker primary puncture-rows, punctures brown to almost black (fig. 5). First primary puncture-row with about 30 punctures. Secondary puncture-rows fine. Brown, sometimes vague markings on the even intervals, on the apical point and along the apical $\frac{2}{3}$ of the suture, median spot connected to the suture.

Ventral side. – Body yellow-brown to yellow-red, prosternal process partly dark-brown, elytral epipleura yellow, legs yellow-brown with some darkening around the coxae and trochanteres. Prosternal process flat, slightly impressed apically, narrowed near the front coxae, strongly punctured (fig. 7), laterally completely bordered (fig. 8). Metasternal process furrowed, deep pit in the middle, strongly punctured (fig. 7). Setiferous striole on dorsal face of hind tibia with about 6 punctures, longer of the two tibial spurs almost as long as the first tarsal segment (fig. 6).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 9-11.

Distribution (fig. 305)

Iraq, Iran?. Alfieri (1976) gives Egypt.

Remarks

This species is described here on the basis of a single female (lectotype) and two male specimens, which are considered to belong to this species (figs. 3-11). It is probably a very variable species, which often may be confused with *variegatus*. There is a good chance that a number of the middle eastern specimens, in literature cited as *variegatus* belong to *abbreviatus*.

Material examined. – 3 ex. – Iraq: 1 ♀ (lectotype). – Iran(?): 1 ♂, Turcom, Kurd., 15943, Millingen, Fry Coll. (BMNH) – Without locality: 1 ♂, Reitter (NHMW).

2. *Haliplus andalusicus* Wehncke

(figs. 12-20)

Haliplus andalusicus Wehncke, 1874: 135. Lectotype ♂ (here designated), [Spain] 'Andalusia, Dieck, Dr. Guignot visité 1925' (MNHN) [examined].

Haliplus andalusicus; Marseul 1882: 107, Seidlitz 1887: 30, Escalera 1914: 57, Scholz 1916: 17, Zimmermann 1920: 303, 1924: 136, Guignot 1933: 232, 1947: 52, 1959: 35, Burmeister 1939: 214, Lagar Mascaró 1968: 73, Hoch 1972: 251, Ienistea 1978: 294.

Diagnosis

This species is most easily confused with *variegatus* from which it can be distinguished by the interrupted lateral plicae of the prosternal process and the apical spur of the hind tibia being as long as or longer than the first tarsal segment.

Description

Length 2.5-3.0 mm, width 1.4-1.7 mm. Body oval, widest in the middle (fig. 12).

Head. – Yellow-brown with usually brown vertex, sparsely punctured. Distance between the eyes $1.9-2.0 \times$ eye-width. Antennae (fig. 13) and palpi yellow to yellow-brown.

Pronotum. – Yellow to yellow-red. Lateral borders straight to slightly convex, finely bordered. Sparsely to rather strongly punctured, basal punctures slightly widened and darkened (fig. 12).

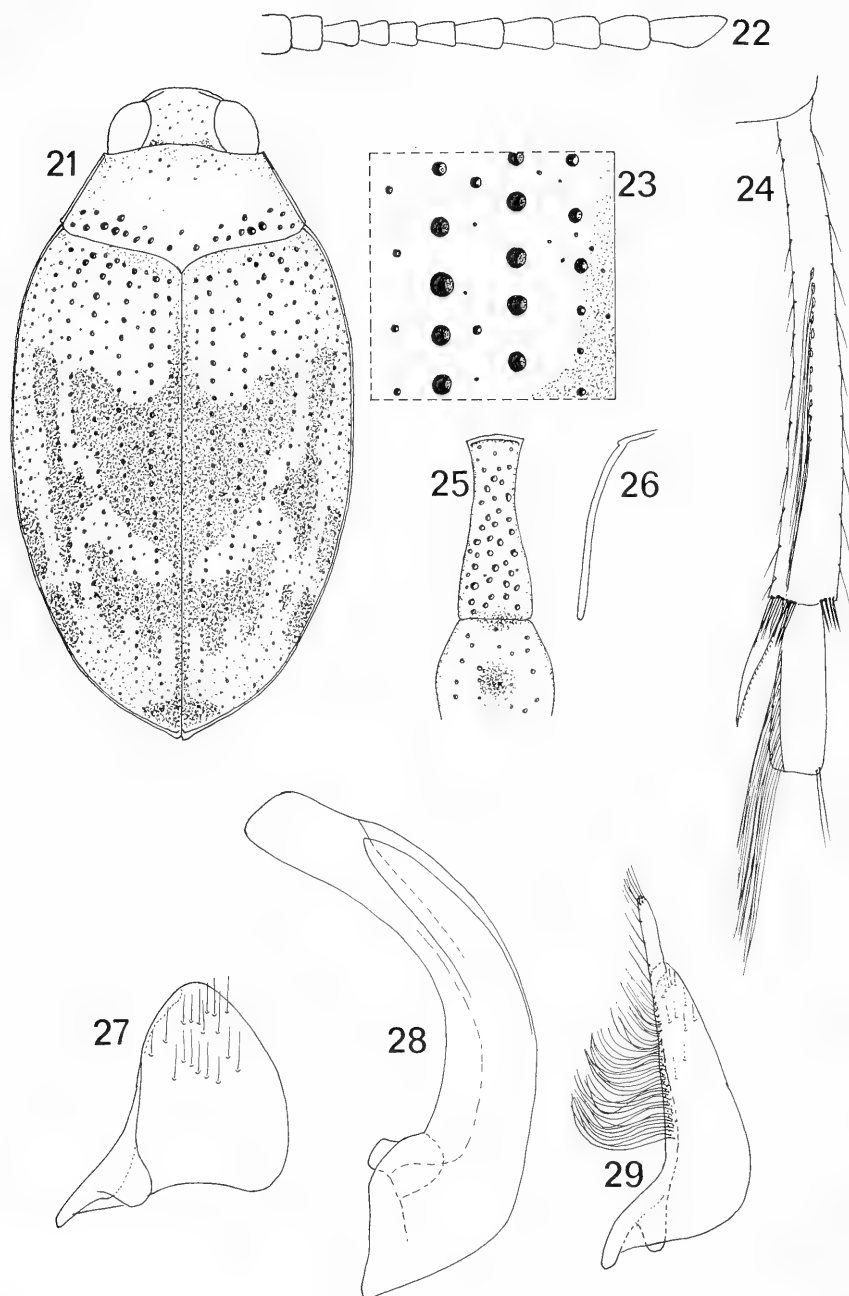
Elytra. – Yellow to yellow-red, primary puncture-rows rather weak with exception of the stronger punctures in the anterior half of the first three rows, 32-36 punctures in the first row (fig. 14). Secondary punctures weak. Darkening of the punctures not always visible. Brown to almost invisible markings on the even intervals, on the apical point and along the apical $\frac{2}{3}$ of the suture, the median spot may be connected to the suture.

Ventral side. – Body yellow to yellow-brown, elytral epipleura yellow, legs yellow-brown. Prosternal process impressed in the middle, strongly punctured, narrowed near the coxae (fig. 16), lateral plicae interrupted before the coxae (fig. 17). Metasternal process grooved with a pit in the middle to largely impressed, sparsely punctured (fig. 16). Setiferous striole on dorsal face of hind tibia with 4-8 punctures, longer of the two tibial spurs as long as or longer than the first tarsal segment (fig. 15).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 18-20.

Biology

In fresh and especially brackish stagnant water in pools near the coast and more rarely inland.



Figs. 21-29. *Haliplus angusi*, holotype. – 21, dorsal view; 22, antenna; 23, elytral punctation; 24, dorsal side of hind tibia; 25, prosternal process; 26, lateral view of prosternal process; 27, left paramere; 28, penis; 29, right paramere.

Distribution (fig. 298)

South of France, Spain (Burmeister 1939, gives The Balears), Morocco, Algeria, Tunisia.

Material examined. – 38 ex. – France: 1 ♀, La Capelle [dep. Lozère], 30.vi.1987 (Leblanc); 6 ex., Albaron, Camargue, A. Chobaut; 1 ex., Montpellier, Et. Laragne, V.M. Duchon (MNH). – Spain: 1 ♂ (lectotype); 1 ♂ (paralectotype), Malaga, Sammlung Cl. Müller (ZSMC); 1 ex., Gibraltar; 1 ex., Palencia (BMNH). – Morocco: 4 ♂, Tanger, Rolph (BMNH). – Algeria: 2 ex., Massif des Mouzaia (BMNH); 4 ex., Philippeville, A. Thery (NHMW, MNHN); 1 ex., Biskra, surroundings, de Vauloger; 1 ex., Biskra, Mertu[?]; 2 ex., no further data (NHMW). – Tunisia: 2 ♂, Gafsa (NHMW); 2 ♂, 1 ♀, 3 ex., surroundings Gafsa, de Vauloger (NHMW, MNHN); 2 ex., Southern Tunisia, iii.iv.1925, ex coll. J. Omer Cooper (BMNH). – Locality unknown: 2 ♂ (paralectotypes), ex. coll. Wehncke (MNH).

3. *Haliphus angusi* sp. n. (figs. 21-29)

Type material. – Holotype ♂, USSR, Siberia, 28.v-28.vi.1982, Novosibirsk oblast, Karasuk, 53.5 N, 78 E, R. B. Angus (ZMAS).

Diagnosis

This species can be distinguished from related ones by the very narrow prosternal process. Possibly there is material in collections representing this species, but identified as *H. maculatus* Motschulsky.

Description

Length 3.3 mm, width 1.7 mm. Body oblong, subparallel, widest in the middle (fig. 21).

Head. – Yellow-red, dark mark on vertex, weakly and sparsely punctured. Distance between the eyes $1.6 \times$ eye-width. Antennae yellow (fig. 22), palpi yellow.

Pronotum. – Yellow to yellow-brown on the disc. Lateral borders straight, lateral margin clearly finer anteriorly. Strongly darkened, occasionally widened punctures along the base, anteriorly rather weakly punctured, otherwise almost unpunctured. Along the central part of the base slightly impressed (fig. 21).

Elytra. – Pale yellow, primary puncture-rows moderately strong, about 33 punctures in the first row (fig. 23). Secondary punctures in the first interval almost as strong as the primary punctures, other secondary punctures rather weak, accompanied by small punctures (fig. 23). Extensive markings: a large arrow-shaped blotch on the disc, on the suture and the apex, often connected oblong blotches in the even intervals. The basal margin, normally covered by the pronotum, yellow-brown till the fifth striae (fig. 21).

Ventral side. – Yellow to yellow-red, elytral epipleura pale-yellow, abdominal segment brown bordered, legs yellow with some darkening near the coxae. Prosternal process narrow, flat, narrowed near the coxae, coarsely punctured (fig. 25), lateral plicae complete (fig. 26). Metasternal process flat with a pit in the middle, sparsely punctured (fig. 25). Coxal plates sparsely and weakly punctured, near the suture almost unpunctured. Setiferous striae on dorsal side of hind tibia over $\frac{1}{2}$ of the tibia length, with about 10 punctures, longer of the two tibial spurs $\frac{3}{4} \times$ the length of the first tarsal segment (fig. 24).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 27-29.

Etymology. – This species is named after the collector Dr. Robert Angus.

Distribution (fig. 304)

Only known from the type-locality: USSR, Siberia, Novosibirsk oblast, Karasuk.

4. *Haliphus astrakhanus* sp. n. (figs. 30-38)

Type material: Holotype ♂, [USSR, Astrakhan] 'Astracan, Koltze' (MNH, Wehncke collection).

Diagnosis

This species is closely related to *ortali*, but in the males the top of the penis is narrower and more pointed.

Description

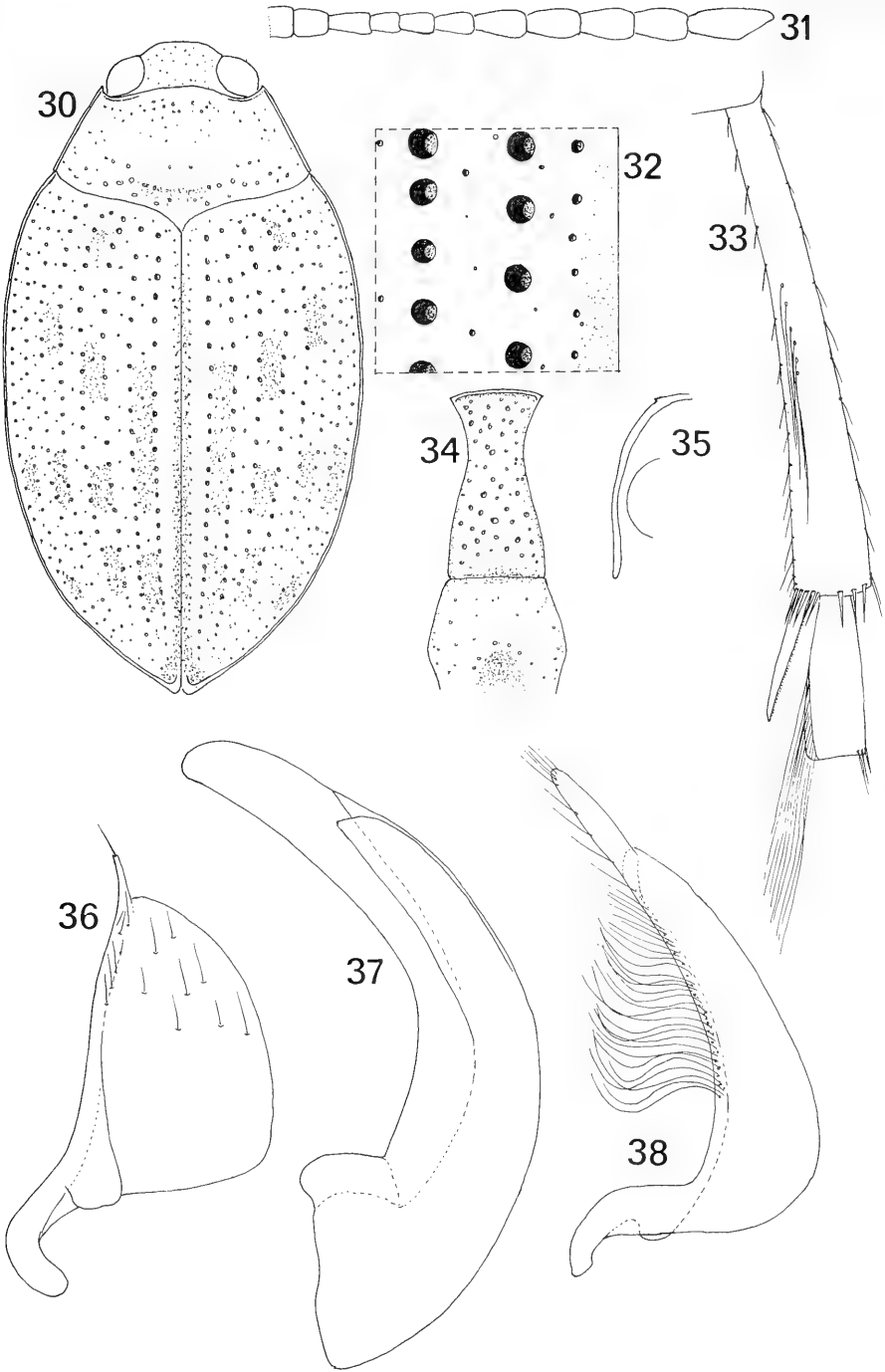
Length 3.4 mm, width 1.9 mm. Body oval, widest in the middle (fig. 30).

Head. – Red-brown, weakly punctured, vertex little stronger punctured. Distance between the eyes $1.5 \times$ eye-width. Antennae (fig. 31) and palpi yellow-red.

Pronotum. – Yellow-red, slightly darker on the disc and along the base. Lateral borders straight, finely bordered. Anteriorly partly bordered. Width $1.8 \times$ the length in the middle. The middle of the base slightly impressed. Weakly punctured, along the base a row of stronger not or hardly darkened punctures (fig. 30).

Elytra. – Yellow-red, many longitudinal vague blotches on the even intervals and along the suture (fig. 30). Primary puncture-rows moderately strong, about 28 punctures in the first row. Secondary punctures weak, accompanied by very small ones (fig. 32). All punctures darkened.

Ventral side. – Yellow-red to red-brown, elytral epipleura yellow, legs yellow-red, darkened to-



Figs. 30-38. *Haliplus astrakbanus*, holotype. – 30, dorsal view; 31, antenna; 32, elytral punctuation; 33, dorsal side of hind tibia; 34, prosternal process; 35, lateral view of prosternal process; 36, left paramere; 37, penis; 38, right paramere.

wards the coxae. Prosternal process flat, moderately strongly punctured, slightly narrowed near the coxae (fig. 34), lateral plicae complete (fig. 35). Metasternal process with a pit in the middle, weakly punctured (fig. 34). Setiferous striole $\frac{1}{6} \times$ the tibia length, with about 6 weak punctures, longer of the two tibial spurs $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 33).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and paramere as in figs. 36–38, left paramere with a small solid parallel digitus, top of penis narrow and a little pointed.

Etymology. – Named after the type locality.

Distribution (fig. 304)

Only known from the type-region Astrakhan in the south-west of the USSR.

5. *Haliphus basinotatus* Zimmermann

(figs. 39–47)

Haliphus basinotatus Zimmermann, 1924: 137. Lectotype ♂ (here designated), [USSR] 'Nikolsk Ussurijsk, Ussuri geb. Mandl, R. Mouchamps det. 62, *Haliphus basinotatus* Zimm., Cotype' (ISNB) [examined].

Haliphus basinotatus ssp. *latiusculus* Nakane, 1985a: 63. Holotype ♂, Yoshii, Fukuoka Pref., Kyushu, Japan, 10.vii.1957, N. Gytoku leg. [not examined].

Haliphus basinotatus; Zimmermann 1924: 137, Zaitsev 1953: 75, Nakane 1985a: 63.

Haliphus basinotatus ssp. *latiusculus*; Nakane 1987: 30.

Diagnosis

This species can be distinguished from related species by the dark basal band on the elytra and its large size. The Japanese subspecies *latiusculus* should differ from the continental form by having 'the front margin of pronotum not or scarcely rounded-produced forwards and the punctuation and elytral pattern appearing somewhat different' (Nakane 1985a).

Description

Length 3.5–4.0 mm, width 1.9–2.1 mm. Body widest just behind the well pronounced shoulders (fig. 39).

Head. – Yellow to yellow-red, vertex usually darkened and nearly unpunctured, frons punctured. Distance between the eyes $1.3\text{--}1.4 \times$ eye-width. Antennae (fig. 40) and palpi yellow-brown.

Pronotum. – Yellow to yellow-red, front margin somewhat darkened or with a small brown blotch. Lateral borders slightly concave to slightly convex with very fine margins. In the anterior part with strong and dense punctures, basal punctures not wider than elytral punctures (fig. 39).

Elytra. – Yellow to yellow-red with distinct brown to nearly black markings on the intervals, along the suture, on the apex and along the base until the sixth puncture-row. The median spots are connected to the suture, but other spots can also show connections (fig. 39). Primary punctures strong, 28–31 punctures in the first row. Secondary punctures fairly strong. All punctures darkened (fig. 41).

Ventral side. – Body yellow to yellow-red, legs yellow to yellow-red, darkened towards the brown trochanteres and coxae. Prosternal process flat, strongly and densely punctured and narrowed near the coxae (fig. 43), laterally with complete plicae (fig. 44). Metasternal process flat, in the middle behind the coxae with a shallow pit (fig. 43), moderately punctured. Setiferous striole on dorsal face of hind tibia with 11–20 punctures, sometimes in a strong groove making the separate punctures hardly recognizable, longer of the two tibial spurs about $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 42).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 45–47.

Distribution (fig. 311)

Easternmost parts of the USSR (near Vladivostok), North Korea, Japan (ssp. *latiusculus*, according to Nakane 1985).

Material examined. – 5 ex. – USSR: 1 ♂, 1 ♀ (lectotype and paralectotype) (ISNB). – North Korea: 2 ♀, 29.vii.1956, M. Magyar, Ch'ongjin (Tshondtsin) (ISNB); 1 ex., Tumen-ula, Russia/Korea border, 14.vii.1913 (ZMUC).

6. *Haliphus chinensis* Falkenström

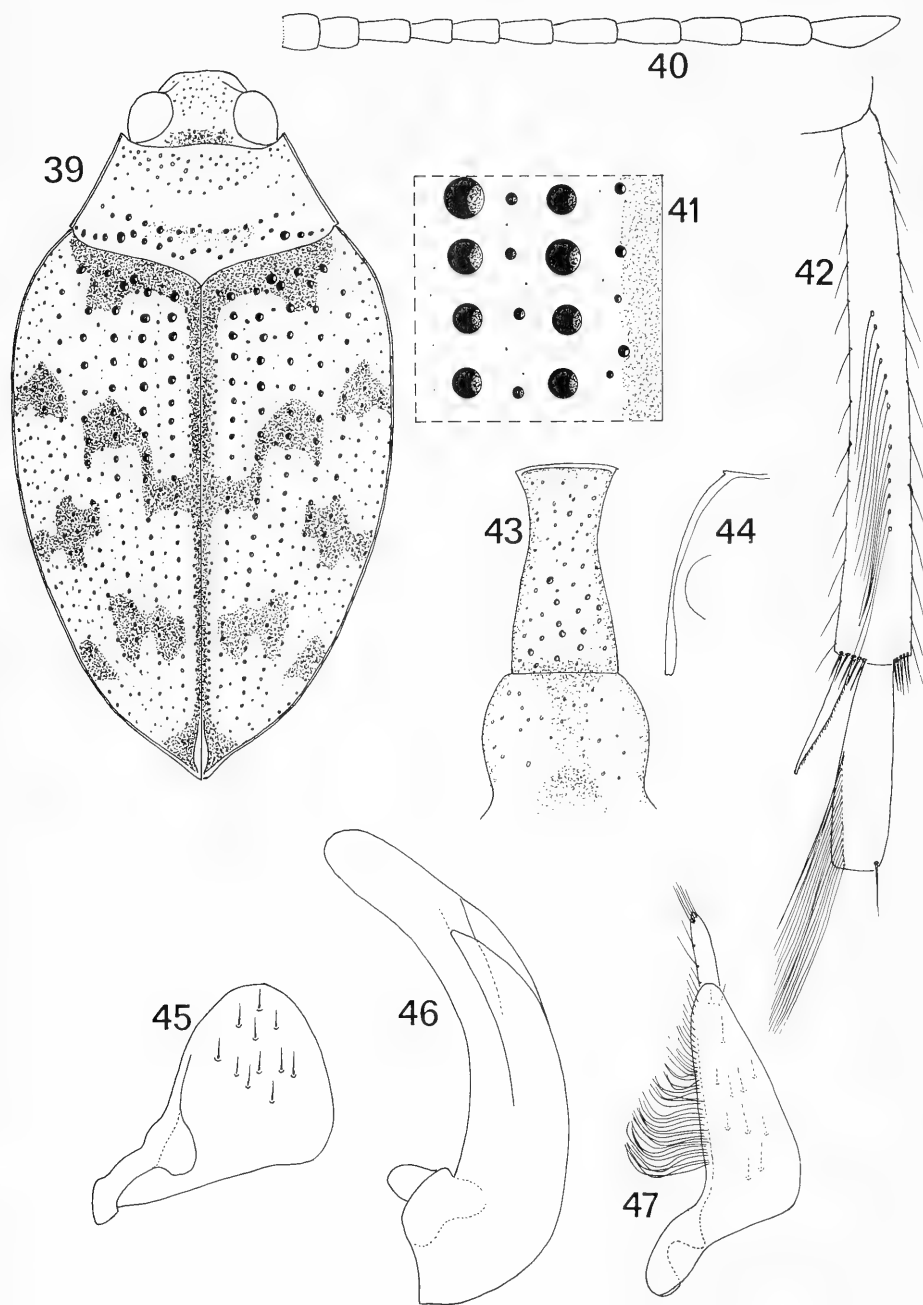
(figs. 48–56)

Haliphus chinensis Falkenström, 1932: 191. Holotype ♀, 'China, N. O. Sichuan, Sven Hedins Exp. Ctr. Asien, Dr. Hummel, 22/5, Typus, *Hal. chinensis* n. sp. Typ. det. Falkenström' (NHRS) [examined].

Haliphus chinensis; Falkenström 1933: 4 (again described as n. sp.), Zaitsev 1953: 71 (as *ovalis*) and 76 (as *chinensis*).

Diagnosis

This species is closely related to *ovalis*. It seems that *ovalis* is restricted to Japan, while the continental specimens, usually considered to belong to *ovalis*, seem to be more related to *chinensis*, although only the female holotype of the latter species has the prosternal process slightly impressed. Despite the fact that all *ovalis*-like specimens that



Figs. 39-47. *Haliphus basinotatus*, lectotype. – 39, dorsal view; 40, antenna; 41, elytral punctuation; 42, dorsal side of hind tibia; 43, prosternal process; 44, lateral view of prosternal process; 45, left paramere; 46, penis; 47, right paramere.

I have seen have a flat prosternal process I think that the continental specimens belong to *chinensis*. The division between the two is mainly based on the smoothly curved penis in the continental specimens, while the specimens from Japan have the penis abruptly bent in the apical part.

Description

Length 3.9-4.2 mm, width 2.1-2.2 mm. Body oval, widest in the middle (fig. 48).

Head. – Yellow to yellow-red, dark marking on vertex, weakly punctured, on the vertex with strong punctures. Distance between the eyes 1.4-1.5 × eye-width. Antennae (fig. 49) and palpi yellow-red.

Pronotum. – Yellow, lateral borders straight, finely bordered. Densely, on the disc sparsely punctured, basal punctures widened and darkened, sometimes only slightly.

Elytra. – Yellow. Suture, apical point and 9 or 10 blotches dark, central blotch on first and third interval sometimes connected to the suture (fig. 48). Primary punctures moderately strong, about 32-36 punctures in the first row. Secondary punctures fairly strong, apically almost as strong as the primary punctures. All punctures darkened (fig. 50).

Ventral side. – Body yellow to yellow-red, elytral epipleura yellow, legs yellow-red, slightly darkened towards the coxae. Prosternal process flat to clearly depressed in the middle of the apical part, strongly and densely punctured, narrowed near the coxae (fig. 52), lateral plicae complete (fig. 53). Metasternal process flat with a pit in the middle, rather weakly punctured (fig. 52). Setiferous striole on dorsal face of hind tibia about half of the tibia length, consisting of about 14 punctures, longer of the two tibial spurs $\frac{2}{3}$ × the length of the first tarsal segment (fig. 51).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 54-56.

Distribution (fig. 309)

China, provinces of Sichuan, Shanxi, Jiangsu, Yunnan.

Remarks

Sato (1984) mentioned a subsp. *sinicus* Balfour-Browne, but the description is unknown to me.

Material examined. – 18 ex. – China: 1 ♀, Holotype ♀ (NHRS); 1 ♂, 1 ♀, Nanjing, v.1928, J. G. Needham (ISNB); 1 ♂, 1 ♀, (Kiangau), C. F. Wu (OLML); 1 ♂, 1 ♀, 1 ex., Shanghai; 1 ex., Yunnan Sen, Excoffier, 1898 (MNHN); 4 ♂, Kelan Pt. (1 ex. labelled as type of subsp. *sinicus* Balfour-Browne) (BMNH, MNHN); 5 ex., Xinjiang (Chin-kiang) (SMFD).

7. *Haliplus dalmatinus* Müller

(figs. 57-69)

Haliplus dalmatinus Müller, 1900: 113. Lectotype ♂ (here designated), [Yugoslavia, Knin] 'Kistanje, Müller D., Museo Civico di Trieste' (MSNT) [examined].

Haliplus dalmatinus var. *Weberi* Müller, 1900: 114. Lectotype ♂ (here designated), [Yugoslavia] 'Mostarsko blato, TYPUS, Museo Civico di Trieste' (MSNT) [examined].

Haliplus dalmatinus; Zimmermann 1920: 307, 1924: 37, Bertrand 1928: 87, Scholz 1929: 16, Guignot 1933: 241, Burmeister 1939: 212, Zaitsev 1953: 71, Gueorguiev 1958: 44, Franciscolo 1972: 63, Ienistea 1978: 294.

Haliplus dalmatinus var. *Weberi*; Zimmermann 1920: 308, 1924: 37, Bertrand 1928: 87, Scholz 1929: 16, Guignot 1933: 241, 1947: 51.

Diagnosis

This species is closely related to *fulvus*, but the latter has shorter metatarsi, a more narrowed prosternal process, in the males a longer digitus on the right paramere and generally a larger size.

Description

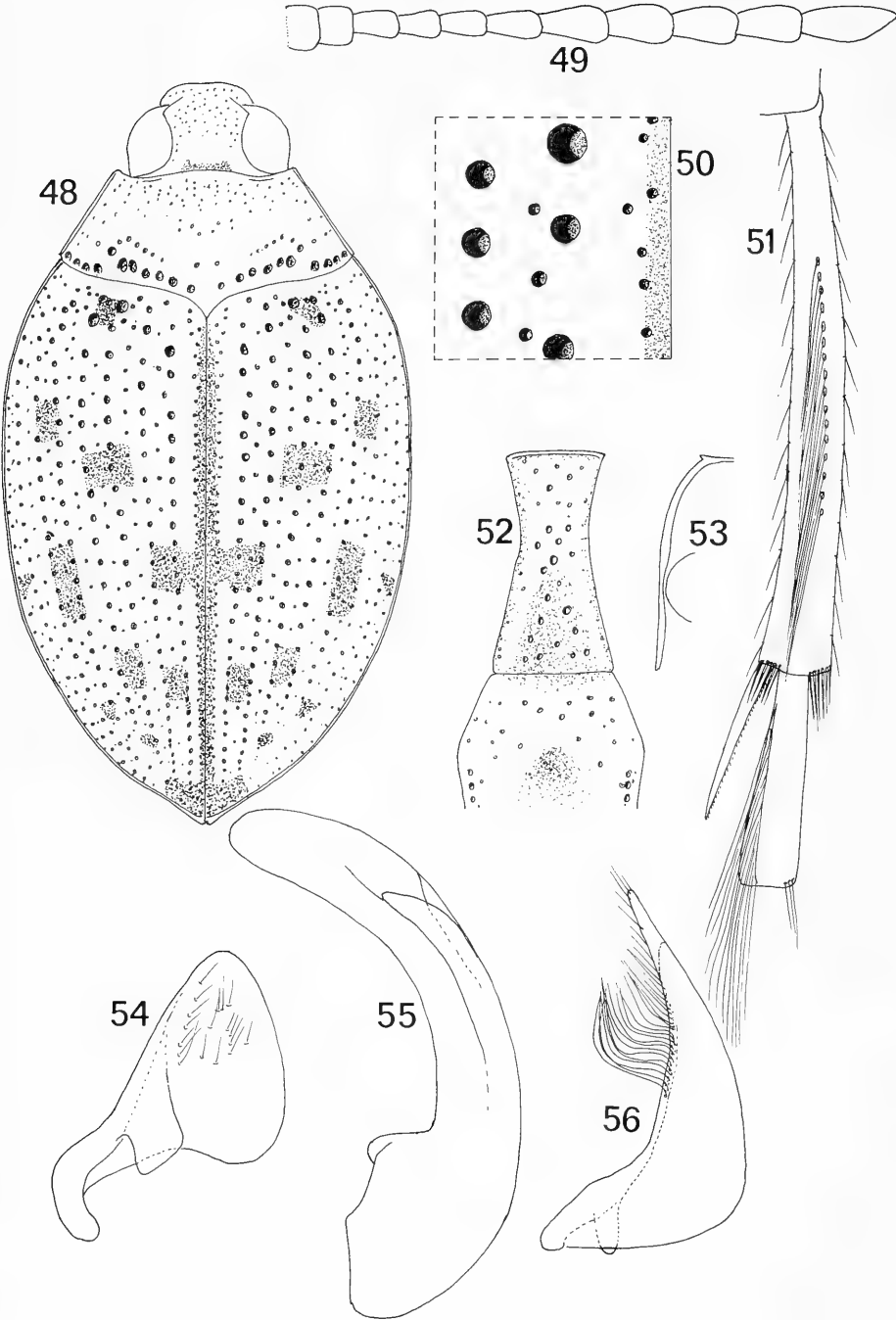
Length 3.2-3.9 mm, width 1.8-2.2 mm. Body oval, sides somewhat parallel, widest in the middle (fig. 57).

Head. – Yellow-red with dark vertex, weakly and sparsely, behind the eyes stronger and more densely punctured. Distance between the eyes 1.4-1.7 × eye-width. Antennae (fig. 58) and palpi yellow-red.

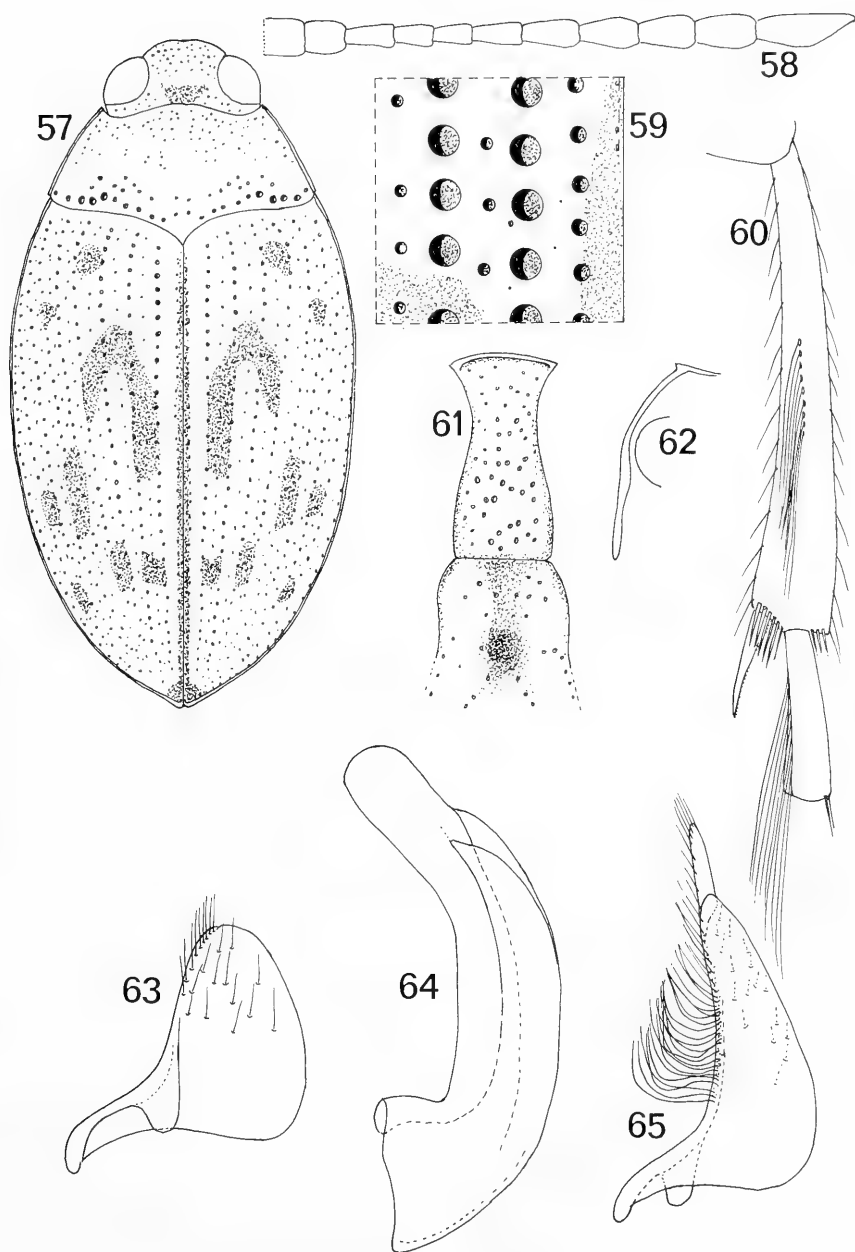
Pronotum. – Yellow, lateral borders straight to slightly convex, finely bordered, except in the middle fairly strongly punctured, basally with a row of widened punctures, basal and discal punctures darkened.

Elytra. – Yellow with variable pattern of brown blotches in the even intervals, sometimes connected to each other, most of the suture and apex darkened (figs. 57, 66-69). Fairly strong primary puncture-rows, about 30 punctures in the first row. Secondary punctures relatively strong. All punctures darkened (fig. 59).

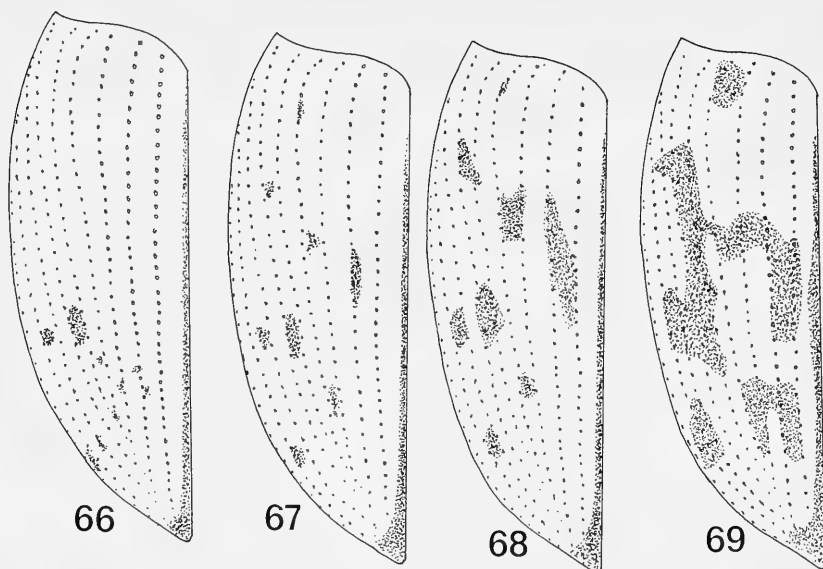
Ventral side. – Body yellow-red, elytral epipleura yellow, legs yellow-red to brown towards the coxae. Prosternal process flat, rather strongly punctured, narrowed near the coxae (fig. 61), lateral plicae complete (fig. 62). Metasternal process flat or slightly grooved, shallow pit in the middle, sparsely punctured (fig. 61). Setiferous striole on dorsal face of hind tibia with 4-7 punctures, longer of the two tibial spurs $\frac{1}{2}$ to $\frac{2}{3}$ × the length of the first tarsal segment (fig. 60). Length of hind tarsus 1.3-1.5 × the tibia length, first tarsal segment 1.6-1.7 × the length of the second segment.



Figs. 48-56. *Haliphus chinensis* (48-53, holotype; 54-56, from Nanjing). – 48, dorsal view; 49, antenna; 50, elytral punctation; 51, dorsal side of hind tibia; 52, prosternal process; 53, lateral view of prosternal process; 54, left paramere; 55, penis; 56, right paramere.



Figs. 57-65. *Haliphus dalmatinus*, lectotype. – 57, dorsal view; 58, antenna; 59, elytral punctuation; 60, dorsal side of hind tibia; 61, prosternal process; 62, lateral view of prosternal process; 63, left paramere; 64, penis; 65, right paramere.



Figs. 66-69. *Haliplus dalmatinus*, elytra. – 66, from Kistanje; 67, from Zara; 68, from Knin; 69, from Skutari.

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 63-65, length of distal process of right paramere $\frac{1}{5}$ \times the length of the basal part (fig. 65).

Distribution (fig. 301)

Along the coast of Yugoslavia and Albania, on the island Corfu (Greece), Turkey, Italy? (identification not sure).

Remarks

Since the description of this species various authors have regarded it as a variety of *fulvus*. Some authors considered *dalmatinus* a variety or subspecies of *variegatus*. Although in some cases *dalmatinus* is very hard to distinguish from small specimens of *fulvus* I consider *dalmatinus* a separate species and I regard the var. *weberi* as an occasional aberration. The elytral maculation is very variable and ranges from almost absent to very extended. One of the syntypes of *Haliplus zimmermanni* from Italy might belong to this species. Specimens from Zadar (Zara), labelled as type, are not considered to belong to the syntype-series as this locality is not mentioned in the original description.

Material examined. – 36 ex. – Yugoslavia: 3♂, 2♀ (lectotype and paralectotypes); 3 ex., surr. of Zadar (Zara), Müller, (1 labelled as Typus); 2 ex., Krk (Veglia), Neto-

litzky; 1 ex., Dalmatia, Rab (Arbe), 20.ix.1910 (MSNT); 1 ex. (paralectotype), Knin (Kistanje), Müller D., Dalmatin det. J. Müller m. Cotypus (ZSMC); 1 ♂ (paralectotype), Knin D., Müller, Cotypus; 1 ex., surr. Zadar (Zara), Müller, Cotypus; 1 ♂, Dalmatia; 1 ♂, Dalmatia, Omis (Almissa), v.1911, Schatzm.; 3 ex. (lectotype and paralectotypes of *dalmatinus* var. *weberi*), Mostarsko blato, Typus, *Haliplus* v. *Weberi* (MSNT); 1 ex., Sinj, Dalmatia (NHMW). – Albania: 2 ♂, Shkodër (Skutari), I. See-Ufer; 2 ♂, Vraça near Shkodër (NHMW). – Greece: 1 ex., Kérkira (Corfu), J. Sahlb., 1035, syntype *Haliplus leopardinus* Sahlberg (1900) (ZSMC). – Turkey: 3 ♂, 2 ♀, Yüsekova, 3.vi.1987, M. Jäch; 5 ♂, Kastamonu, 25.vi.1989, M. Jäch (NHMW). – Italy: 1 ♀ (syntype of *Haliplus zimmermanni* Gschwendtner, 1921), Salò, 23.v.1909, Type 1921, det. L. Gschw., Type, *Haliplus* ?*dalmatinus* Müller det. B. J. v. Vondel 1987 (ZSMC).

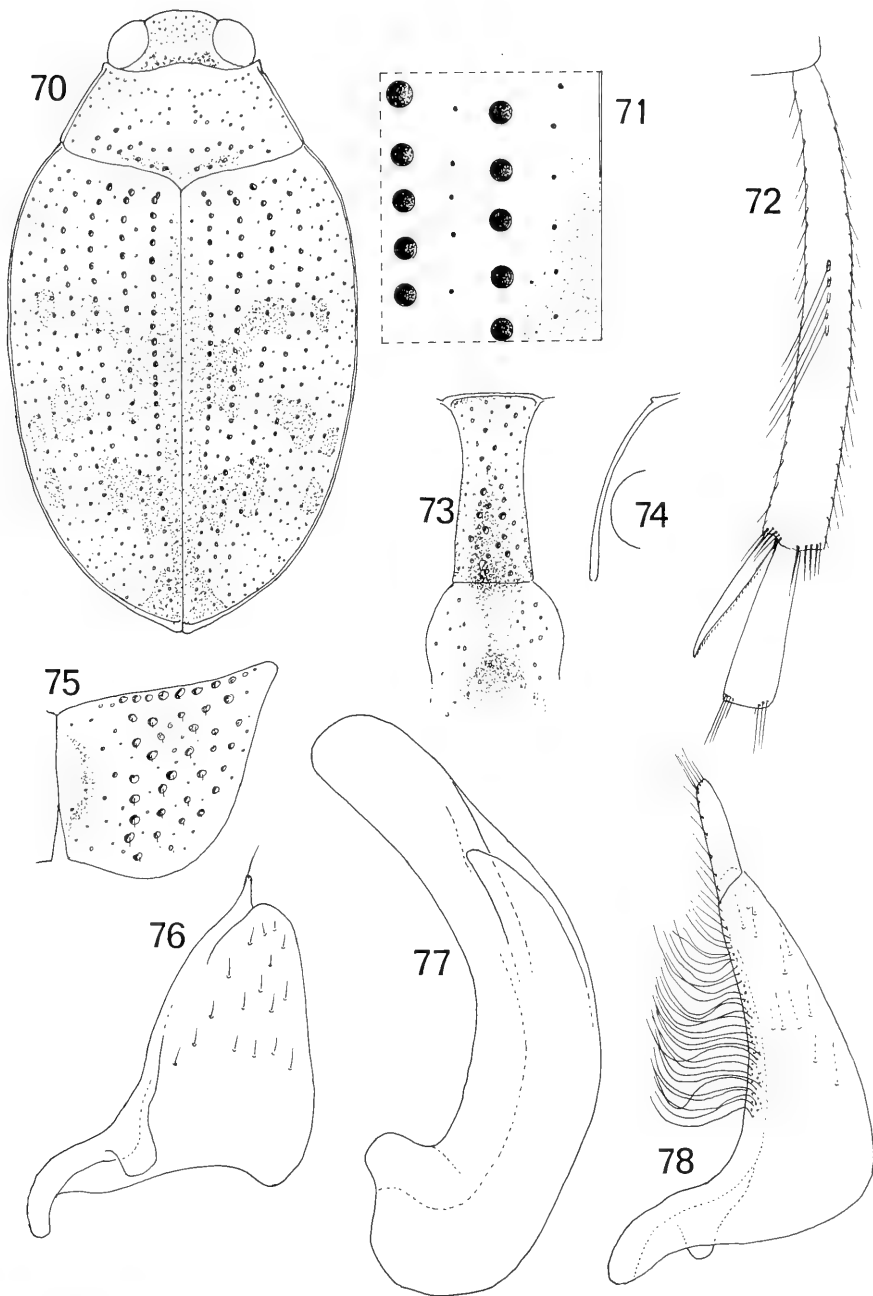
8. *Haliplus davidi* sp. n.

(fig. 70-78)

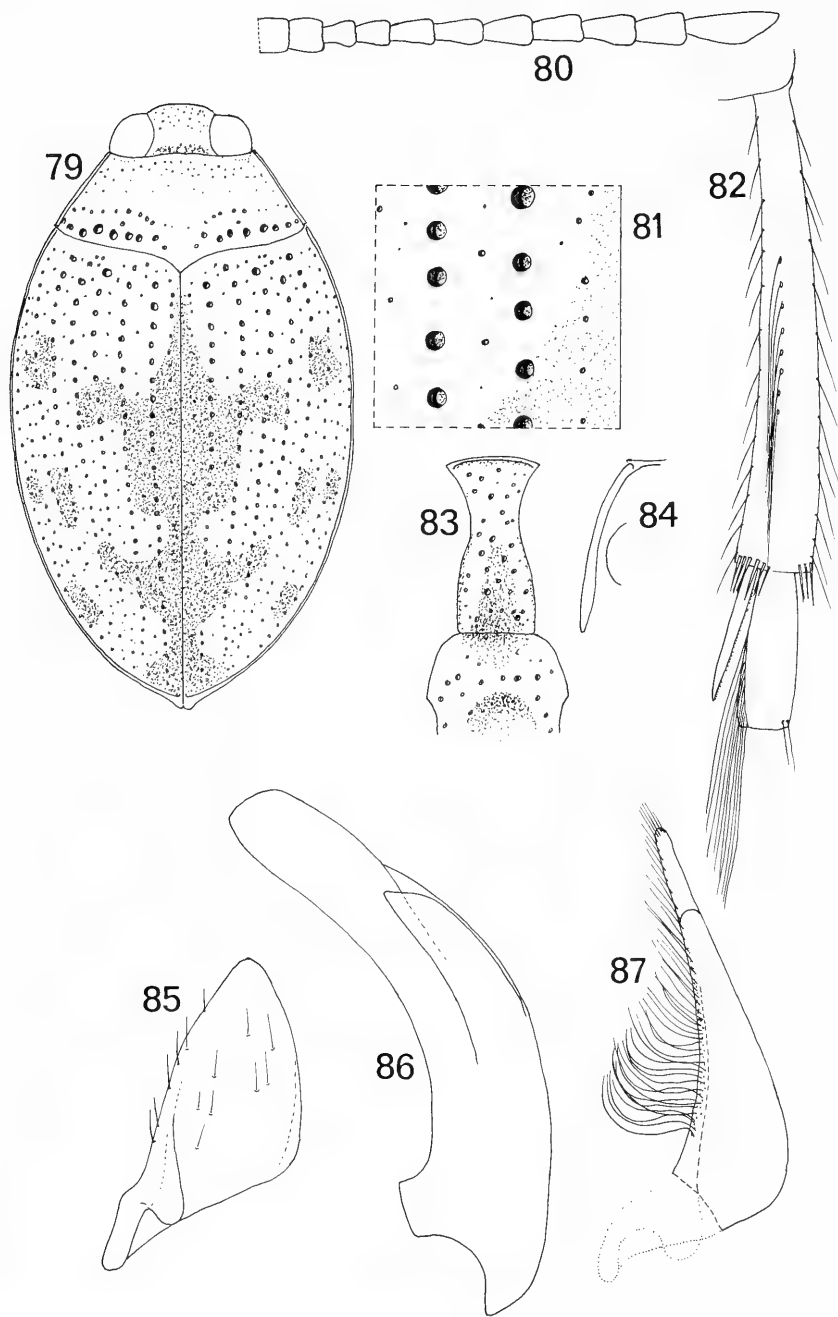
Type material: Holotype ♂, [China, Beijing] 'Nord Pekin, A. David, 1865, Museum Paris, *Haliplus Sharpi* Westw., M. Régimbart det. 1898, 227.65 [round label]' (MNHN); Paratype ♀, China, Yunnan (MNHN); Paratype ♂, Beijing (Peping), C.F. Wu (OLML); Paratype ♂, Heilongjiang (Mandsch.), Harbin, 28.ix.1930, v. Jettmer (ZMHB).

Diagnosis

Male specimens can be distinguished from *diruptus* by the presence of a digitus on the left paramere. I am not always able to separate the females of these species.



Figs. 70-78. *Haliplus davidi*, holotype. – 70, dorsal view; 71, elytral punctuation; 72, dorsal side of hind tibia; 73, prosternal process; 74, lateral view of prosternal process; 75, hind coxal plate; 76, left paramere; 77, penis; 78, right paramere.



Figs. 79-87. *Haliplus diruptus*, holotype. – 79, dorsal view; 80, antenna; 81, elytral punctation; 82, dorsal side of hind tibia; 83, prosternal process; 84, lateral view of prosternal process; 85, left paramere; 86, penis; 87, right paramere.

Description

Length 3.2 mm, width 1.7 mm. Body oval, widest in the middle (fig. 70).

Head. – Yellow-brown, brown blotch on vertex, densely punctured, unpunctured band between the hind parts of the eyes. Distance between the eyes $1.3 \times$ eye-width. Antennae yellow (missing in holotype), palpi yellow-brown.

Pronotum. – Yellow-brown. Lateral borders straight, clearly bordered. Width at the base $2.0 \times$ the length in the middle and $1.6 \times$ the width in front. Weakly and densely, along the base more strongly punctured, some basal punctures darkened. Beside the middle of the base slightly impressed (fig. 70).

Elytra. – Yellow-brown, with darkened suture and apex and several blotches (fig. 70). Primary puncture-rows moderately strong, wider near the base, basal punctures in the second to fourth row widened, about 35 punctures in the first row. Secondary punctures moderately strong, in some intervals very sparse, accompanied by very small punctures (fig. 71), all punctures darkened.

Ventral side. – Yellow-red to yellow-brown, elytral epipleura yellow, legs yellow-brown, some darkening towards the coxae. Prosternal process at the apex strongly impressed, coarsely punctured, posteriorly little narrower than anteriorly, slightly narrowed near the coxae (fig. 73), lateral plicae complete (fig. 74). Metasternal process grooved and strongly impressed in the middle, rather strongly punctured (fig. 73). Coxal plates strongly and densely punctured, small punctures between the normal ones, which are provided with hairs, along the suture with a weakly punctured area, apical parts of the plates dilated (fig. 75). Setiferous striole $\frac{1}{3}$ of the tibia length, with about 5 punctures, longer of the two tibial spurs $\frac{3}{4}$ the length of the first tarsal segment (fig. 72).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 76-78, left paramere with a short solid digitus.

Etymology. – Named after the collector A. David.

Distribution (fig. 312)

Only known from China: Yunnan, Beijing and Harbin.

9. *Haliphus diruptus* Balfour-Browne (figs. 79-90)

[*Haliphus simplex* sensu Régimbart 1899, nec Clark 1863. Misidentification].

Haliphus diruptus Balfour-Browne, 1946: 436. Holotype

♂ 'China, Tientsin' [Tianjin] 'F. M. Thomson, 1904-229, *Haliphus simplex* Rég., -Zimm., *Haliphus diruptus* nom. nov. J. Balfour-Browne det., 'Type' (BMNH) [examined].

Haliphus simplex; Zimmermann 1924: 136, Takizawa 1931: 142, Zaitsev 1953: 74, Sato 1960: 252, 1984: 2, Cho 1969: 167, Yoon 1988: 621.

Haliphus diruptus; Guignot 1954: 563.

Diagnosis

A very variable species. Specimens with and without black blotches or bands on the base of the elytra and specimens with weak or with very strong and close punctures on the head are considered to belong to this species. Specimens with a very reduced and weakened maculation resemble *davidi*, from which males can be distinguished by the lack of a small solid digitus on the left paramere, but distinguishing females can be problematic.

Description

Length 2.8-3.5 mm, width 1.6-2.0 mm. Body oval, widest in the middle (fig. 79).

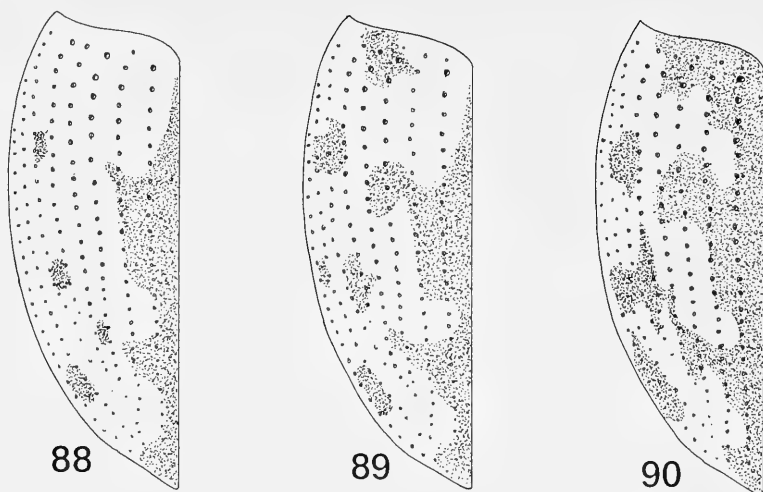
Head. – Yellow to yellow-brown, vertex slightly darkened, punctuation weak and fairly sparse to strong and dense. Distance between the eyes $1.3-1.5 \times$ eye-width. Antennae (fig. 80) and palpi yellow-red.

Pronotum. – Yellow to yellow-red. Lateral borders straight to slightly convex, finely bordered. Punctures moderately strong to strong along the base and in the anterior central part, basal and anterior punctures darkened, remaining punctures sometimes darkened.

Elytra. – Yellow to yellow-brown, variable maculation: darkening along suture and on apex, a central blotch on the suture and small blotches on the even intervals; in extreme forms the maculation can be very extended and includes a large blotch or even a complete band along the base (figs. 88-90). Primary punctures moderately strong, first row slightly weaker than second to fourth or even fifth row, 30-40 punctures in the first row. Secondary punctures moderately strong, rows consisting of normal and very small ones, sometimes very strong along suture. All punctures darkened (fig. 81).

Ventral side. – Body yellow to yellow-brown, elytral epipleura yellow, legs yellow to yellow-brown, slightly darkened near the coxae. Prosternal process clearly impressed in the apical part, strongly narrowed near the front coxae (fig. 83), lateral plicae complete (fig. 84), fairly strongly punctured. Metasternal process flat with a pit in the middle, sparsely punctured (fig. 83). Setiferous striole on dorsal face of hind tibia about $\frac{1}{3} \times$ the tibia length, containing about 8 punctures, longer of the two tibial spurs about $\frac{3}{4} \times$ the length of the first tarsal segment (fig. 82).

Figs. 88-90. *Haliplus di-ruptus*, elytra. – 88, from Beijing; 89, 90, from Tonkin.



Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 85-87.

Distribution (fig. 311)

Easternmost part of China, provinces of Hebei, Heilongjiang, Hunan and Jiangsu. Extreme south-eastern part of the USSR: Maritime Territory. Vietnam. Guignot (1954) gives Burma, Shan State.

Material examined. – 81 ex. – China: 1 ♂, Holotype; 1 ♀ (paratype), Tianjin (Tientsin), vi.1902, F. M. Thomson; 1 ♂, Harbin, 25.viii.1952 (BMNH); 1 ♂, 1 ♀, Beijing (Peping), C. F. Wu (OLML); 1 ♂, 1 ♀, Tianjin (Tientsin) (SMFD); 1 ex., Tianjin (Tien-Tsin); 1 ex., Beijing (Nord Pekin), A. David 1865; 4 ex., Shanghai; 1 ex., Hengshan (Hontsang), Weber; 1 ♂, (Zi-ka-wei) (MNHN); 1 ex., Yangzhou (Yang Chow Ku), 20.vi.1947, Sunabricotier (ISNB); 1 ♂, Beijing (Peping), C. F. Wu (OLML). – Korea: 1 ex., 11.vii.1956, M. Magyar, Sariwon, Type, *Haliplus sharpi* var. *homologus* n. var. cf. texte, R. Mouchamps det. 63 [unpublished name] (ISNB). – Vietnam: 62 ex., Tonkin, Hoa Binh region, vii.1940 (part of material), A. de Cooman (ISNB, MNHN). – Without locality: 1 ex. (MNHN).

10. *Haliplus excoffieri* sp. n.

(fig. 91-101)

Type material: Holotype ♂, [China] 'Yunnan-Sen, Mgr Excoffier, 1898, Dr. Régimbt vidit 1898, Museum Paris ex coll. Oberthür'. Paratypes: 1 ♂, 3 ♀, same data (MNHN).

Diagnosis

This species is closely related to *chinensis* and *ovalis*, but the distance between the eyes is usually

less than $1.4 \times$ eye-width, the darkened suture is only reaching to the first secondary puncture-row and in the males the penis is clearly widened before the apex.

Description

Length 3.7-3.8 mm, width 1.9-2.0 mm. Body oblong oval, tapering apically, widest in or just before the middle (fig. 91).

Head. – Brown, dark marking on vertex, rather densely punctured, unpunctured band between the hind parts of the eyes. Distance between the eyes $1.2-1.4 \times$ eye-width. Antennae yellow to yellow-brown (fig. 92), palpi yellow-brown.

Pronotum. – Yellow to yellow-brown, lateral borders straight, clearly bordered. Width at the base about $2.0 \times$ the length in the middle and $1.6 \times$ the width in front. Sparsely, anteriorly densely, basally strongly punctured, on the disc almost unpunctured. About ten of the darkened basal punctures widened, sometimes slightly impressed along the central part of the base (fig. 91).

Elytra. – Yellow to yellow-brown, suture darkened until the secondary puncture-row, dark blotches on the apex and in mainly the even intervals. Primary puncture-rows moderately strong, second to fourth puncture-row getting stronger basally, 32-36 punctures in the first row. Secondary puncture-row along the suture rather weak, but very dense in the apical half, on the other intervals sometimes relatively strong (fig. 93). All punctures darkened.

Ventral side. – Yellow to yellow-red, elytral epipleura yellow, legs yellow-brown, darkened towards the coxae. Prosternal process slightly convex, strongly narrowed near the coxae, densely

punctured (fig. 96), lateral plicae complete (fig. 97). Metasternal process flat, strong impression in the middle, weakly punctured (fig. 96). Coxal plates strongly punctured, along the suture weakly punctured (fig. 98). Hind margins of fifth and sixth abdominal segment with complete double puncture-rows (fig. 98). Setiferous striole almost half of the tibia length, with about 10 groove-like connected punctures, longer of the two tibial spurs $\frac{2}{3}$ the length of the first tarsal segment, tibia $3 \times$ the length of the first tarsal segment (fig. 95).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on the ventral side. Penis and parameres as in figs. 99–101.

Etymology. – This species is named after the collector Mgr J. C. Excoffier.

Distribution (fig. 312)

Only known from China, Yunnan-province.

11. *Haliphus eximis* Clark (figs. 102–110)

Haliphus eximis Clark, 1863: 418. Syntypes, Korea, Clark (depository unknown; probably in SAMA or MAMU).

Haliphus modestus Zimmermann, 1924: 139. Holotype ♂, 'Sumatra, Type, Holotype Staatssamml. München' (ZSMC) [examined]. Syn. n.

Haliphus biogoensis Kano & Kamiya, 1931: 1. Types burned during World War II (Dr. T. Nakane, pers. comm.) [not examined].

Haliphus emmerichi Falkenström, 1936: 79. Holotype ♀, [Kangdin, Sichuan] 'Nitou Tatsienlu, Szechuan China', Typus, *Haliphus Emmerichi* Falk. ♀, det. Falkenström' (NHRS) [examined].

[*Haliphus flavicollis*; auctt., nec Sturm 1834: Wu 193:342. Misidentification].

Haliphus eximis; Zimmermann 1920: 305, 1924: 132, Takizawa 1931: 140, Guignot 1950: 97, Zaitsev 1953: 77, Cho 1969: 166, Sato 1984: 2, Nakane 1985a: 63, 1985b: 40, 1987: 29, Yoon 1988: 623.

Haliphus modestus; Zimmermann 1927: 2.

Haliphus biogoensis; Sato 1984: 2, Nakane 1985b: 40.

Haliphus emmerichi; Guignot 1950: 97, Zaitsev 1953: 69, Sato 1984: 2.

Diagnosis

This species can be distinguished from related species in the East Palaearctic and Oriental region by the total lack of maculation between the elytral puncture-rows. It resembles the West Palaearctic *flavicollis*, which however lacks the lateral plicae in the anterior part of the prosternal process.

Description

Length 3.4–3.9 mm, width 1.9–2.1 mm. Body oval, widest in or just before the middle (fig. 102).

Head. – Yellow-brown to rust-coloured, mode-

rate weakly punctured. Distance between the eyes $1.3\text{--}1.4 \times$ eye-width. Antennae (fig. 103) and palpi yellow-brown.

Pronotum. – Yellow to rust-coloured. Lateral borders straight to slightly convex, bordered, basally wider than base of elytra, strongly tapering anteriorly. Width $2.1\text{--}2.2 \times$ the length in the middle. With strong punctures except on the unpunctured disc, basal punctures partly widened, basal and anterior punctures darkened.

Elytra. – Yellow to rust-coloured. Strong primary puncture-rows, about 32 punctures in the first row. Secondary punctures relatively strong, as dense and apically almost as strong as the primary punctures (fig. 104). Except for the partly darkened suture, no markings present.

Ventral side. – Yellow, sternites yellow-brown, legs yellow-brown to rust-coloured. Prosternal process broad and flat, slightly narrowed near the coxae, strongly punctured (fig. 106), lateral plicae complete (fig. 107). Metasternal process flat with a pit in the middle, sparsely punctured (fig. 106). Setiferous striole on dorsal face of hind tibia with about 12 punctures, longer of the two tibial spurs $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 105).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 108–110.

Distribution (fig. 308)

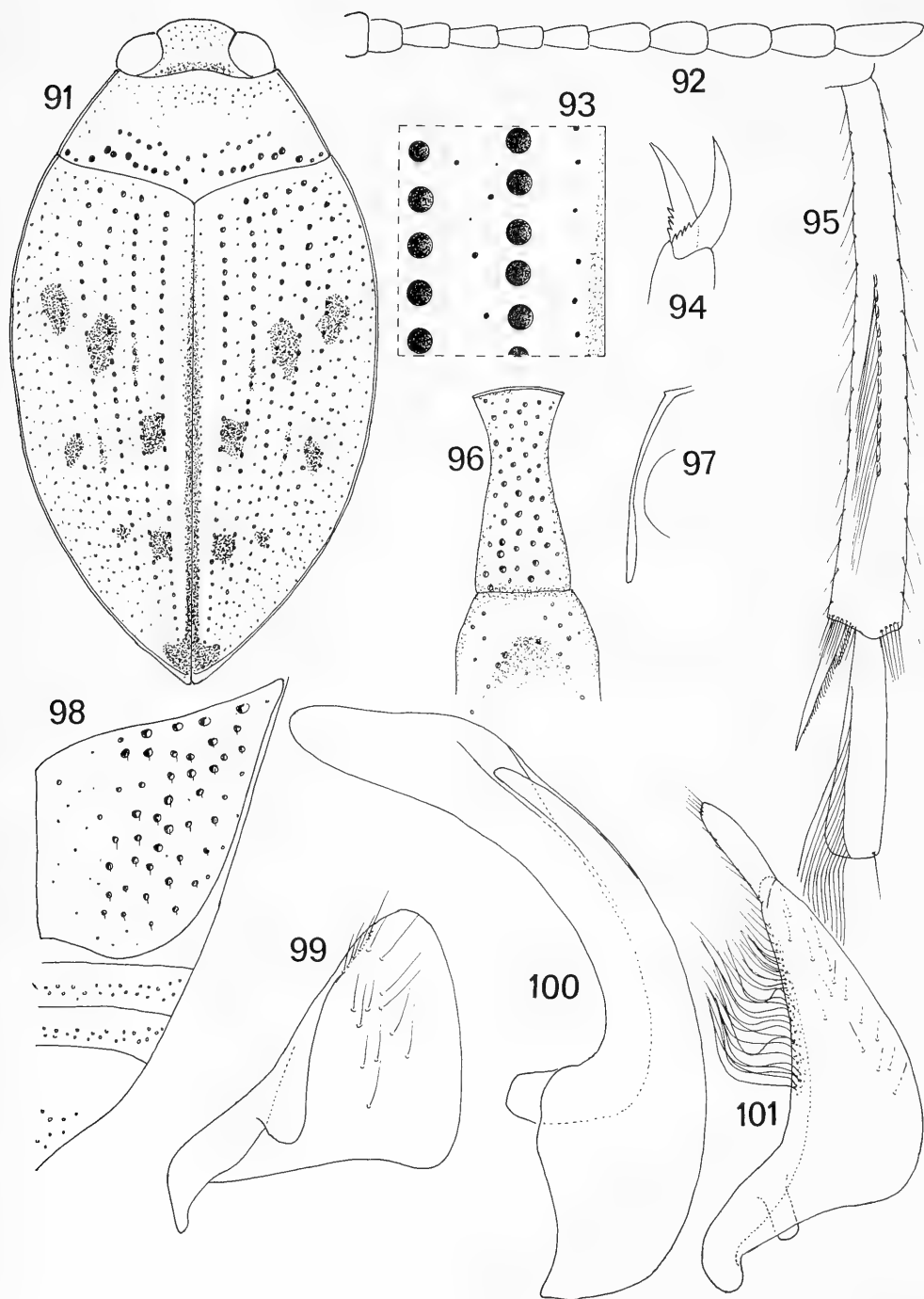
China (prov. Sichuan, Xinjiang, Zhejiang, Zaitsev (1953) gives Shanghai), Korea, Japan (Honshu, Kyushu), Vietnam, Sumatra.

Remarks

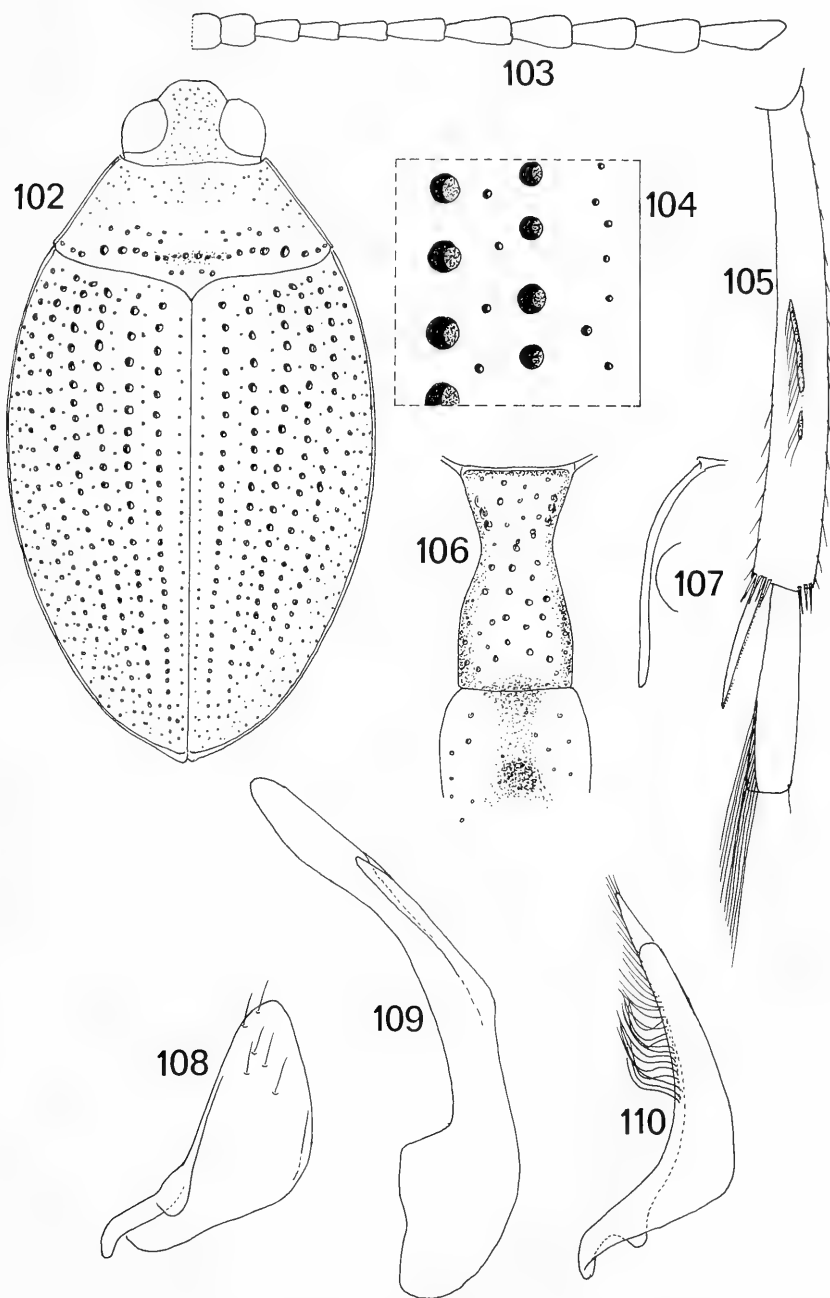
The specimen from China, present in BMNH and labelled as Type of *eximis*, does not belong to Clark's two syntypes, described from Korea. The holotype of *modestus*, described from Sumatra is here considered conspecific with *eximis*.

Material examined. – 16 ex. – China: 1 ♂, Type (BMNH); 1 ex., Kiangau, C. F. Wu (OLML); 1 ♀, Holotype *Haliphus emmerichi* (NHRS); 4 ex., North-west. China, Xinjiang (Chinkiang), Cotypus (SMFD); 1 ♂, Zhejiang, Zhoushan (Chekiang, Chusan), 15.iv.1931 (MNHN). – Japan: 10 ex., Aobadai, Aira I, Kagoshima Pref., 26.ix.1985. E. Matsui (Vondel). – Korea: 1 ex., Tshou-Bon San, 1.vii.1956, M. Magyar (ISNB). – Vietnam: 6 ex., Tam Dao, Tonkin, H. Perrot; 1 ex., Tonkin, Hoa Binh, iii.1940, A. de Cooman (ISNB). – Indonesia: 1 ♀, holotype of *modestus* (ZSMC).

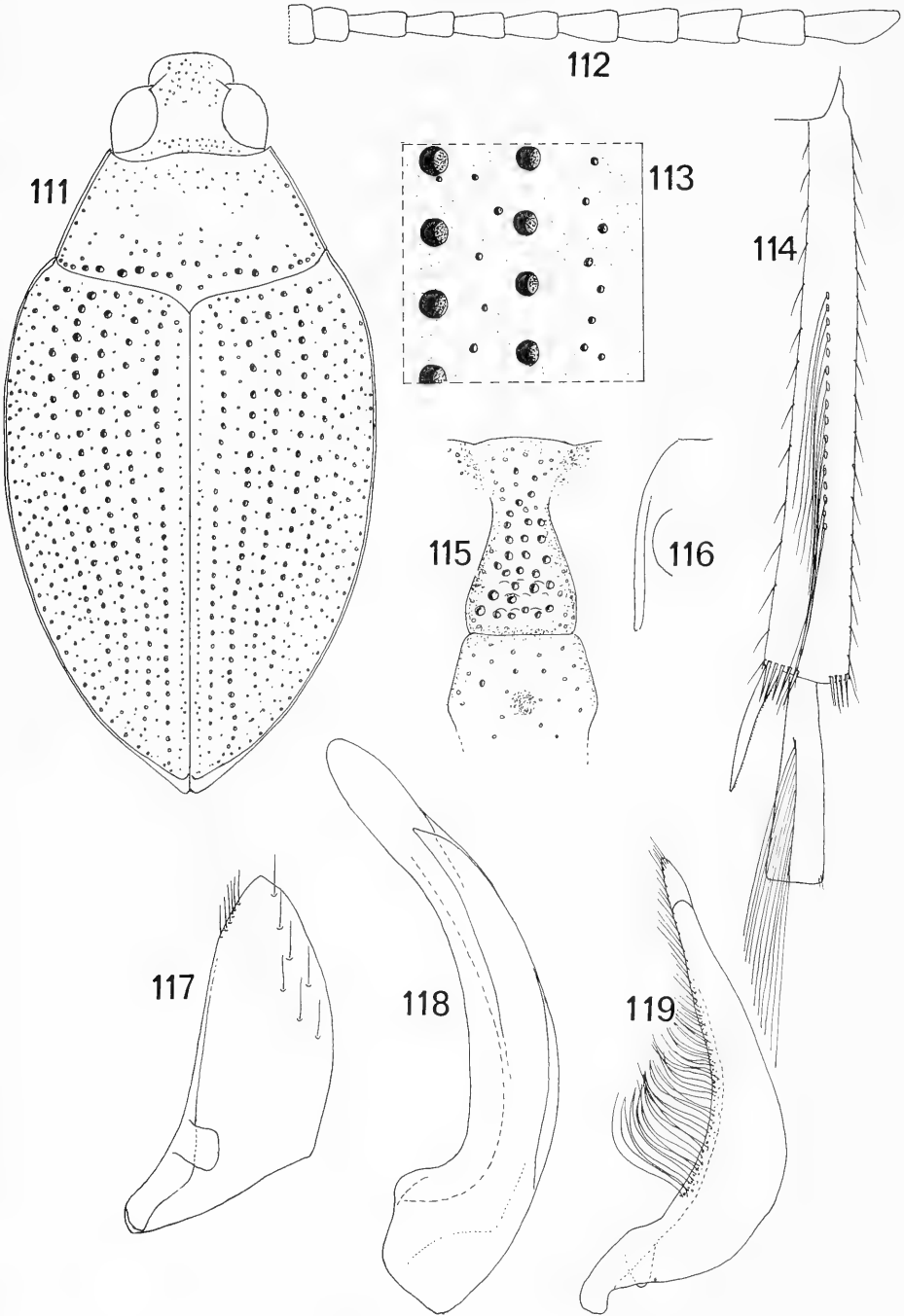
12. *Haliphus flavicollis* Sturm (figs. 111–119)



Figs. 91-101. *Haliplus excoffieri*, holotype. – 91, dorsal view; 92, antenna; 93, elytral punctuation; 94, fore claws; 95, dorsal side of hind tibia; 96, prosternal process; 97, lateral view of prosternal process; 98, hind coxal plate and sternites; 99, left paramere; 100, penis; 101, right paramere.



Figs. 102-110. *Haliplus eximis*, China. – 102, dorsal view; 103, antenna; 104, elytral punctuation; 105, dorsal side of hind tibia; 106, prosternal process; 107, lateral view of prosternal process; 108, left paramere; 109, penis; 110, right paramere.



Figs. 111-119. *Haliphus flavicollis*, Hendrik Ido Ambacht, Netherlands. – 111, dorsal view; 112, antenna; 113, elytral punctuation; 114, dorsal side of hind tibia; 115, prosternal process; 116, lateral view of prosternal process; 117, left paramere; 118, penis; 119, right paramere.

- Haliphus flavicollis* Sturm, 1834: 150. Types not located, probably lost as most of the Sturm-types [not examined].
- [*Haliphus ferrugineus*; sensu auctt., nec Linnaeus, 1767. Misidentification].
- [*Haliphus impressus*; sensu auctt., nec Fabricius, 1787. Misidentification].
- Haliphus flavicollis* var. *pallida* Semenov, 1904: 202. Types probably in ZMAS [not examined].
- Haliphus flavicollis* var. *expallidus* Zaitsev, 1907: 122 (Replacement name for *pallida* Semenov).
- Haliphus unicolor* Fiori, 1914: 188. Types not located [not examined].
- Haliphus flavicollis*; Aubé 1836: 24, 1838: 12, Schaum 1848: 42, Thomson 1854: 183, Seidlitz 1887: 31, Müller 1900: 115, Apfelbeck 1904: 361, Fiori 1904: 196, Zimmermann 1920: 305, 1924: 132, Guignot 1928: 143, 1933: 230, 1947: 50, Kinel 1929: 219, Scholz 1929: 15, Kolossov 1931: 116 (var. *ruskyi* Stange, nom. nud.), Balfour-Browne 1936: 75, 1938: 12, 1940: 148, 1951: 1, 1953: 5, F. Burmeister 1939: 212, E. Burmeister 1982: 94, 1987: 184, Csiki 1946: 559, Zaitsev 1953: 68, Gueorguiev 1960: 23, Lindroth 1960: 42, Freude 1971: 15, Seeger 1971a: 409, 1971b: 532, 1971c: 165, Franciscolo 1972: 61, 1979: 117; Jackson 1973: 253, Ienistea 1974: 208, 1978: 294, Minorsky & Dzumailo 1974: 26, Galewski 1976: 31, Konev 1976: 56, Mateleshko 1977: 68, Fichtner 1981: 327, Holmen 1981: 2, 1987: 114, Leblanc 1984: 8, Lundberg 1986: 11, Zakharenko & Moroz 1988: 283, Belyashevskiy 1989: 124, Vondel 1989a: 58, 1989b: 17.
- Haliphus flavicollis* var. *expallidus*; Zimmermann 1920: 305, Guignot 1933: 239, Zaitsev 1953: 68.
- Haliphus unicolor*; Burmeister 1939: 214.

Diagnosis

This species is related to *eximis* and *rubidus*. From *eximis* it can be distinguished by the lack of lateral plicae in the anterior part of the prosternal process. In *rubidus* the basal elytral punctures are larger than the distance between the punctures of the first and second row in the basal part, while in *flavicollis* these punctures are clearly smaller than that distance. In specimens from Morocco, however, that difference is less clear. The males of *flavicollis* have the left paramere narrower at the base than in *rubidus*.

Specimens with vague blotches on the elytra can be distinguished from *fulvus* by the lack of the lateral plicae in the anterior part of the prosternal process.

Description

Length 3.6-4.1 mm, width 1.8-2.1 mm. Body fairly slender, sometimes subparallel, widest before the middle (fig. 111).

Head. – Yellow to rust-coloured, sparsely punctured. Distance between the eyes 1.4-1.6 × eye-width. Antennae (fig. 112) and palpi yellow to yellow-red.

Pronotum. – Yellow to rust-coloured. Lateral

borders straight, finely bordered. Sparsely, anteriorly and basally more densely punctured, basal irregular puncture-row about as strong as basal elytral punctures. All punctures usually black (fig. 111).

Elytra. – Yellow to rust-coloured, strong primary puncture-rows, about 32 punctures in the first row. Secondary rows with relatively strong and between them very weak punctures (fig. 113). All punctures black. Suture weakly darkened, no clear markings on the intervals, sometimes vague blotches on the apical half.

Ventral side. – Body yellow to yellow-brown, elytral epipleura yellow, legs yellow-brown, femora darkened basally, trochanters dark. Prosternal process flat, wide apically, strongly narrowed near the coxae (fig. 115), lateral border without plicae before the coxae (fig. 116), strongly and densely punctured. Metasternal process flat with a strong impression in the middle, sparsely punctured (fig. 115). Setiferous striole on dorsal face of hind tibia long and grooved, separate punctures hardly recognizable, longer of the two tibial spurs about $\frac{2}{3}$ × the length of the first tarsal segment (fig. 114).

Male sexual characters. – First three tarsal segments of fore- and midlegs hardly widened laterally, slightly widened ventrally, scaly hairs on ventral side. Penis and parameres as in figs. 117-119.

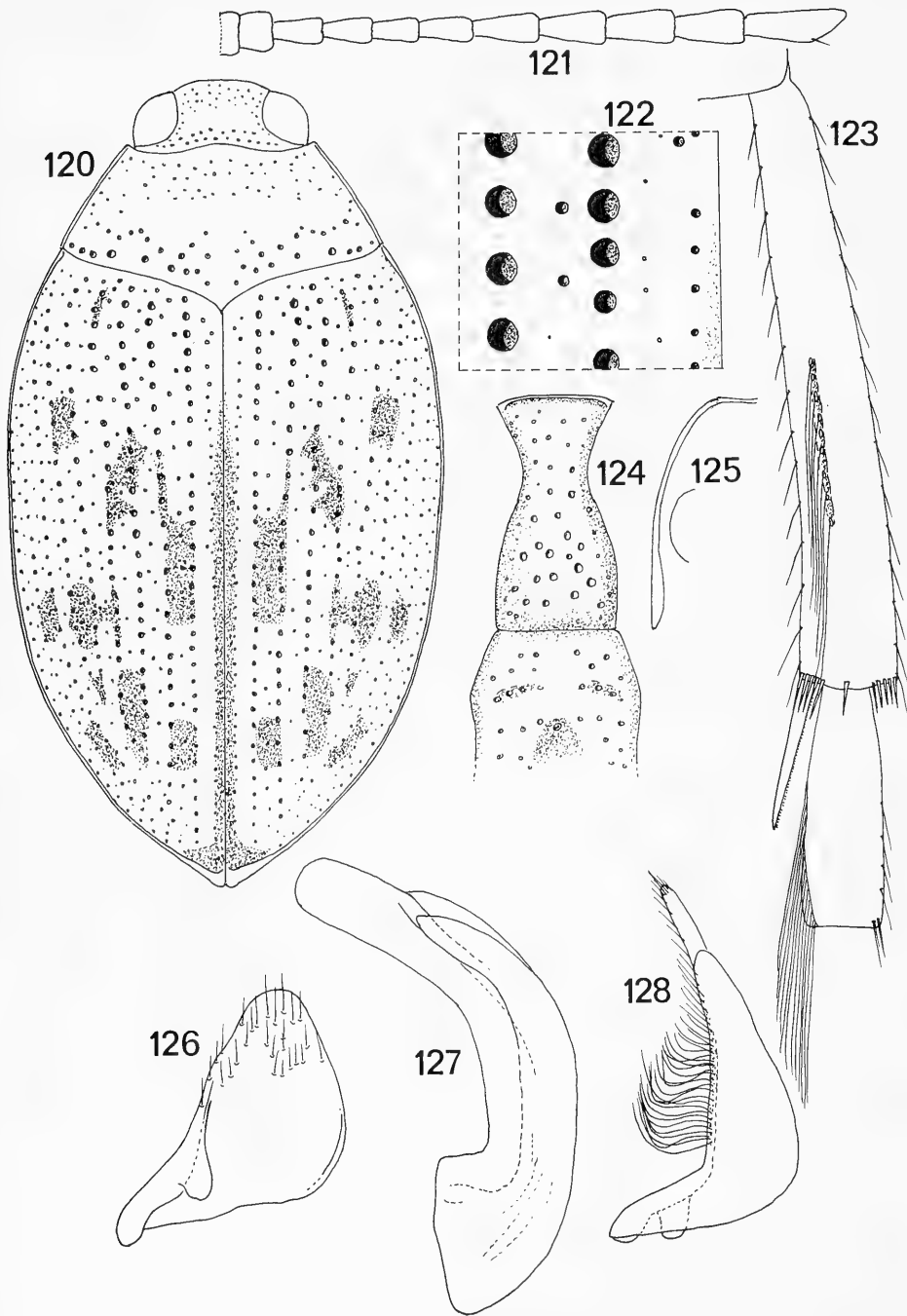
Female: Elytra completely and very densely covered with micropunctures.

Biology

In clean and clear stagnant or very slowly running water of lakes, ditches, canals and pools with rich vegetation, especially Characeae (Seeger 1971c), Najadaceae (Burmeister 1939) or *Cabomba*-beds in Kazakhstan (Konev 1976). Also recorded from brackish water. The adults feed on eggs and larvae of *Chironomidae* (Seeger 1971c), aquatic macro-invertebrates as *Asellus* (only when dead or dying), *Sialis* larvae (probably predated), dead waterbeetles, even of their own species and probably Characeae or filamentous algae. Seeger (1971a, b, c) provided much information on the life-cycle. The egg has been described by Seeger (1971a), the 2nd and 3rd-stage larvae and the pupa have been described by Bertrand (1928). This species is able to fly (Jackson 1973, taken at light).

Distribution (fig. 295)

All Europe except the north of Norway, the utmost north of Sweden, the north of Finland, Iceland, Spain and Portugal. Turkey. USSR: European part, Western Siberia except the extreme north, Transcaucasia, Kazakhstan, China (Guignot 1947), Mongolia. Records from Morocco probably concern specimens of *rubidus*, which is not always



Figs. 120-128. *Haliphus fulvus*, Gars, Austria. – 120, dorsal view; 121, antenna; 122, elytral punctuation; 123, dorsal side of hind tibia; 124, prosternal process; 125, lateral view of prosternal process; 126, left paramere; 127, penis; 128, right paramere.

easy to distinguish from *flavicollis*. Egypt? (Holmen 1987). Ali (1976) records specimens of *fulvicollis* from Iraq, but according to the characters he used in his identification-key he obviously meant *flavicollis*.

Material examined. – 881 ex. – Austria: 97 ex. (CNCI, NHMW, ZMAN, RMNH). – Belgium: 7 ex. (RIN, RMNH, Jongema). – Czechoslovakia: 20 ex. (NHMW, RMNH). – France: 23 ex. (CNCI, NHMW, RIN, RMNH, Jongema, Vondel). – Germany: 24 ex. (NHMW, ZMAN, RMNH). – Great Britain: 9 ex., (CNCI, BMNH, ZMAN, Vondel). – Greece: 2 ex. (ZMAN). – Hungary: 2 ex. (CNCI). – Ireland: 1 ex. (BMNH). – Italy: 4 ex. (CNCI, Jongema, RMNH, NHMW). – Luxembourg: 1 ex. (ZMAN). – Mongolia: 1 ♂, Üür Gol, 28.ix.1897, Frenzel (ZMHB). – Netherlands: 649 ex. (ZMAN, MOG, FNML, NHMR, RIN, RMNH, Berge Henegouwen, Cuppen, Drost, Hielkema, Huybregts, Jongema, Onder de Linden, Schilthuizen, Vallenduuk, Vondel). – Poland: 13 ex. (NHMW, RMNH). – Rumania: 1 ex. (RMNH). – Switzerland: 8 ex. (ZMAN, Rotzer). – USSR: 1 ex., Panfilov, Kazakhstan; 1 ex., Kiyev, Ukraine, 27.ix.1988, M. Jäch (NHMW). – Locality not traced or unknown: 17 ex. (BMNH, NHMW, RMNH).

13. *Haliphus fulvus* (Fabricius) (figs. 120-131)

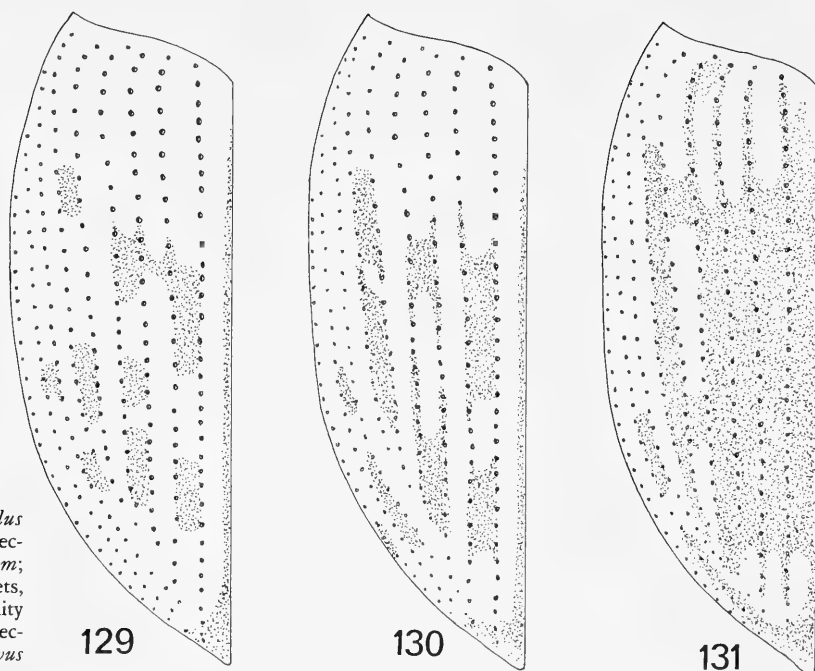
Dytiscus fulvus Fabricius, 1801: 271. Types not located, probably lost (Zimsen 1964: 70) [not examined].
Dytiscus interpunctatus Marsham, 1802: 429. Lectotype ♀ (here designated), *interpunctatus* (BMNH) [examined].
Haliphus lapponum Thomson, 1854: 184. Lectotype (here designated), *H. ferrugineus*, coll. Lund, *H. ferrugineus* Zett., ?syntype (MZLU, Zetterstedt-collection) [examined].
Haliphus pyraeneus Delarouzée, 1857: xcv. Types from Lac Noire near Cauterets (Hautes Pyrénées) are probably in MNHN [not examined]. Material from NHMW, labelled as TYPUS and COTYPUS is collected in 1881 and thus can not belong to the syntype-series.
Haliphus lapponum var. *niger* Seidlitz, 1887: 31. Types not located [not examined].
Haliphus fulvus var. *carlittensis* Régimbart, 1901: 323. Types probably in MNHN [not examined].
Haliphus subguttatus Crotch, 1873: 384. **Syn. n.**
Haliphus fulvus a. *multistriatus* Scholz, 1915: 232. Types not located [not examined].
Haliphus fulvus *Sparre-schneideri* Munster, 1922: 15. Lectotype ♂ (here designated), [Norway, Malselv] 'Bjerkeng, 12.6.97, *H. schneideri* i. lit., *fulv. schneideri* det. Ganglbauer, COTYPUS' (NHMW) [examined].
Haliphus fulvus v. *unicolor* Munster, 1922: 14. Types not located [not examined].
Haliphus salinarius Wallis, 1933: 56. Holotype ♂, [Canada] 'Oyosoo, B.C., V-4-1929' (CNCI) [examined]. **Syn. n.**
[*Haliphus ferrugineus*; sensu auctt., nec Linnaeus, 1767. Misidentification].
Haliphus fulvus; Clairville 1806: 220, Sturm 1834: 148, Babington 1836: 177, Erichson 1837: 183, Thomson 1854: 183, Westhoff 1881: 43, Seidlitz 1887: 31, Ap-

felbeck 1904: 360, Escalera 1914: 57, Zimmermann 1920: 307, 1924: 134, Bertrand 1928: 87, 1949: 25, Guignot 1928: 144, 1933: 230, 1947: 51, Scholz 1929: 16, Balfour-Browne 1936: 74, 1938: 11, 1940: 146, 1951: 4, 1953: 5, Pearce 1939: 34, F. Burmeister 1939: 212, Horion 1941: 365, Brinck 1942: 5, Strand 1944: 122, Csiki 1946: 560, Jackson 1952: 66, 1956: 87, 1973: 253, Zaitsev 1953: 70, Riha 1955: 57, Gueorguiev 1958: 44, 1960: 23, 1981: 401, Lindroth 1960: 42, Lagar Mascaró 1968: 72, Freude 1971: 15, Seeger 1971b: 558, 1971c: 165, Ienistea 1974: 208, 1978: 294, Minoransky & Dzmailo 1974: 26, Alfieri 1976: 38, Galewski 1976: 29, Konev 1976: 56, Gislason 1977: 159, Mateleshko 1977: 68, Franciscolo 1979: 119, Fichtner 1981: 327, Holmen 1981: 2, 1987: 115, Leb-lanc 1984: 40, Lundberg 1986: 11, E. Burmeister 1987: 184, Zakharenko & Moroz 1988: 283, Belyashevskiy 1989: 124, Vondel 1989a: 58, 1989b: 17.
Haliphus interpunctatus; Zimmermann 1920: 307.
Haliphus lapponum; Seidlitz 1887: 31, Zimmermann 1920: 308, Bertrand 1928: 87, 1949: 25, Guignot 1928: 144, 1930: 73, 1933: 231, 1947: 51, Kinell 1929: 219, Scholz 1929: 16, Balfour-Browne 1936: 74 1938: 11, 1940: 147, Burmeister 1939: 213, Pearce 1939: 34, Horion 1941: 365, Brinck 1942: 5, Strand 1944: 122, Zaitsev 1953: 71, Riha 1957: 57, Lagar Mascaró 1968: 72, Ienistea 1978: 294, Lundberg 1986: 11.
Haliphus pyraeneus; Marseul 1882: 106, Zimmermann 1920: 308, Bertrand 1928: 87, Kinell 1929: 219, Scholz 1929: 16, Burmeister 1939: 213.
Haliphus subguttatus; Blatchley 1910: 203, Roberts 1913: 101, Zimmermann 1920: 139, Wallis 1933: 54, 1973: 100, J. Balfour-Browne 1948: 158, Hatch 1953: 192, Ruette 1970: 57, Hilsenhoff & Brigham 1978: 21, White et al. 1985: 357, Larson 1987: 107.
Haliphus lapponum var. *niger*; Scholz 1929: 16, Guignot 1933: 242.
Haliphus fulvus var. *carlittensis*; Zimmermann 1920: 308, Bertrand 1928: 87, Guignot 1928: 144, 1930: 73, 1933: 242, Kinell 1929: 219, Scholz 1929: 16, Burmeister 1939: 213, Pearce 1939: 34.
Haliphus fulvus a. *multistriatus*; Zimmermann 1920: 308, Bertrand 1928: 87, Guignot 1933: 241.
Haliphus fulvus *sparre-schneideri*; Guignot 1933: 241, Strand 1944: 122, Zaitsev 1953: 71, Döbler 1976: 182 (as *schneideri*), Ienistea 1978: 294.
Haliphus fulvus v. *unicolor*; Falkenström 1941: 88.
Haliphus salinarius; Hatch 1953: 192, Ruette 1970: 56, Larson 1987: 107.
Haliphus ferrugineus; Gyllenhal 1808: 546, Zetterstedt 1828: 236, Stephens 1829: 40, Aubé 1836: 22, 1838: 10, Babington 1836: 176, Zimmermann 1920: 308.

Diagnosis

This species is very variable in size, maculation and coloration. Of all Halipilidae it has the largest distribution, covering most of the palaeartic and the north of the nearctic region. Mainly because of the variation in elytral maculation a number of varieties, subspecies and separate species such as *lapponum* (fig. 129) and *pyraeneus* (fig. 130) have been described. A range of intermediate forms between the latter species and *fulvus* has been examined and I can only confirm what other authors like

Figs. 129-131. *Haliplus fulvus*, elytra. – 129, lectotype of *H. lapponum*; 130, from Cauterets, France, the type locality of *H. pyraeneus*; 131, lectotype of *H. fulvus sparre-schneideri*.



Balfour-Browne (1936) and Holmen (1987) already concluded, that they belong to the same species.

Description

Length 3.6-4.5 mm, width 2.0-2.4 mm. Body long oval, widest in the middle (fig. 120).

Head. – Yellow-red, brown or rust-coloured, puncturation weak to moderately strong, between the eyes sparser, behind the eyes stronger and denser punctured. Distance between the eyes 1.6-1.9 \times eye-width. Antennae (fig. 121) and palpi yellow.

Pronotum. – Yellow to rust-coloured. Lateral borders straight to slightly convex, finely bordered. Punctures moderately strong, on the disc almost absent, the basal row widened and slightly to strongly darkened.

Elytra. – Yellow to rust-coloured, very variable pattern of light to dark brown blotches in the even intervals, sometimes the blotches are hardly or not present or they are very strong and then covering nearly the entire elytra (described as *sparre-schneideri*) (fig. 131). Primary punctures moderately strong, sometimes stronger in the basal part. Secondary rows irregular and containing two types of punctures, the usual ones and very fine ones (fig. 122). All punctures darkened.

Ventral side. – Body yellow, yellow-red or rust-

coloured, elytral epipleura yellow, legs yellow to rust-coloured, darkened towards the coxae. Prosternal process flat to slightly convex, narrowed near the coxae (fig. 124), lateral plicae complete (fig. 125), with moderately strong to very strong and dense punctures. Metasternal process flat with a pit in the middle (fig. 124), with moderately strong and dense punctures. Setiferous striole on dorsal face of hind tibia grooved, stretched over about $\frac{1}{3}$ of the length, consisting of 10 to 20 hardly recognizable punctures, longer of the two tibial spurs $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 123). Length of hind tarsus, including claws, about 1.2 \times the tibia length, first tarsal segment 1.5-1.9 \times the length of the second segment.

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 126-128, length of the distal process of the right paramere $\frac{1}{3} \times$ the length of the basal part (fig. 128).

Biology

In clean clear or peaty stagnant or slowly running water of lakes, pools, canals, rivers and ditches with rich vegetation of especially Characeans. Even recorded from brackish water. The larvae probably feed on Characeans such as *Nitella*, while the adults

are omnivorous with a diet of algae, pollen and invertebrates like Oligochaeta (Seeger 1971b). The third-stage larva was first described by Schiødte (1864). The beetle has been seen flying and has been caught at light.

Distribution (fig. 292)

All of Europe, including Iceland. USSR: European part and Siberia as far as Yakutia in the east and Transcaucasia and Kazakhstan in the south. Turkey. North Africa: Morocco, Algeria. The records of Syria (Burmeister 1939) and Iraq (Ali 1976) possibly concern *maculatus*, which is certainly a different species. Canada (states of British Columbia, Alberta, North West Territories, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia and New-Foundland) and northern parts of the United States from west to east, southwards to about 45° N (states of Washington, Idaho, South Dakota, Minnesota, Wisconsin, Indiana and Massachusetts) (until now referred to as *salinarius* and *subguttatus*).

Remarks

Type-material of the nearctic species *subguttatus* sensu Roberts and *salinarius* Wallis has been examined and in my opinion both are conspecific with *fulvus*. For *salinarius* that possibility was already noticed by Holmen (1987). Crotch (1873) mentioned *subguttatus* referring to a Leconte manuscript, but he did not regard it as a separate species, but as a form of *cribarius* Leconte. Blatchley (1910) described it as a subspecies of *cribarius*. Roberts (1913) discovered that *subguttatus* was not conspecific with *cribarius* and described it as a separate species. His holotype is probably in AMNH. Two of his paratypes have been examined (CNCI).

Material examined. – 712 ex. – Austria: 36 ex. (RMNH, NHMW, ZMAN, OLML). – Belgium: 7 ex. (RMNH, RIN, Jongema). – Canada: 3 ex. (holotype and 2 paratypes of *salinarius*); 1 ♂, (paratype of *subguttatus*), Fraz. Val. B.C.; 1 ♂, (paratype of *subguttatus*), Antigonish, N.S. (CNCI); 44 ex. (CNCI, Vondel). – Czechoslovakia: 2 ex. (NHMW, OLML). – Denmark: 1 ex. (NHMW). – Finland: 10 ex. (RMNH, ZMAN, RMNH, NHMW). – France: 30 ex. (RMNH, ZMAN, RMNH, NHMW, BMNH, OLML, Vondel). – Germany: 39 ex. (RMNH, NHMW, ZMAN, BMNH, OLML). – Great Britain: 94 ex. (CNCI, ZMAN, BMNH, Vondel). – Greece: 1 ex. (OLML). – Hungary: 2 ex. (NHMW, ZMAN). – Ireland: 18 ex. (BMNH). – Italy: 3 ex. (CNCI). – Netherlands: 228 ex. (BMNH, ZMAN, FNML, NHMR, NHMW, RIN, RMNH, Cuppen, Drost, Hielkema, Jongema, Onder de Linden, Vondel). – Norway: 38 ex. (RMNH, ZMAN, BMNH, OLML, MZLU, RMNH); 1 ♂, (lectotype of *fulvus* var. *sparre-schneideri*), 1 ♀, (paralectotype of *fulvus* var. *sparre-schneideri*), Bjerkeng, ix.1878, Schneider, *Haliphus Sparre-Schneideri* n. sp., *fulv. Schneideri* det. Ganglbauer, Typus (NHMW). – Poland: 12 ex. (NHMW). – Rumania: 2 ex. (NHMW). – Spain: 1 ex. (Cuppen). – Sweden: 11 (NHMW, ZMAN,

RMNH, BMNH). – USA: 1 ex., Larive Lake, South Dakota, 22.vi.1940 (CNCI). – USSR: 1 ex. (BMNH). – Yugoslavia: 3 ex. (CNCI, OLML). – Locality not traced or unknown: 118 ex. (NHMW, BMNH, MZLU, RMNH, OLML), 1 ex., (♀ lectotype of *interpunctatus*), (BMNH); 1 ex. (lectotype of *lapponum*) (MZLU).

14. *Haliphus gafnyi* sp. n. (figs. 132-140)

Type material: Holotype ♂, Israel, Nesher quarry, 27.i.1989, R. Ortal, IES 5344 (HUJ). Paratypes: 1 ♂, Israel, Berekhat, Nesher quarry, 26.xii.1989, R. Ortal, IES 5502 (Angus); 1 ♂, Cyprus, Zakaki Marshes, ii.1948, G. Mavromoustaki (Angus); 1 ♂, Syria, Damascus (MNH).

Diagnosis

This species resembles *abbreviatus* and *villierii* in a number of characters, but can be distinguished from them by the flat, strongly and densely punctured metasternal process.

Description

Length 2.9-3.1 mm, width 1.5-1.7 mm. Body oblong oval, widest in the middle (fig. 132).

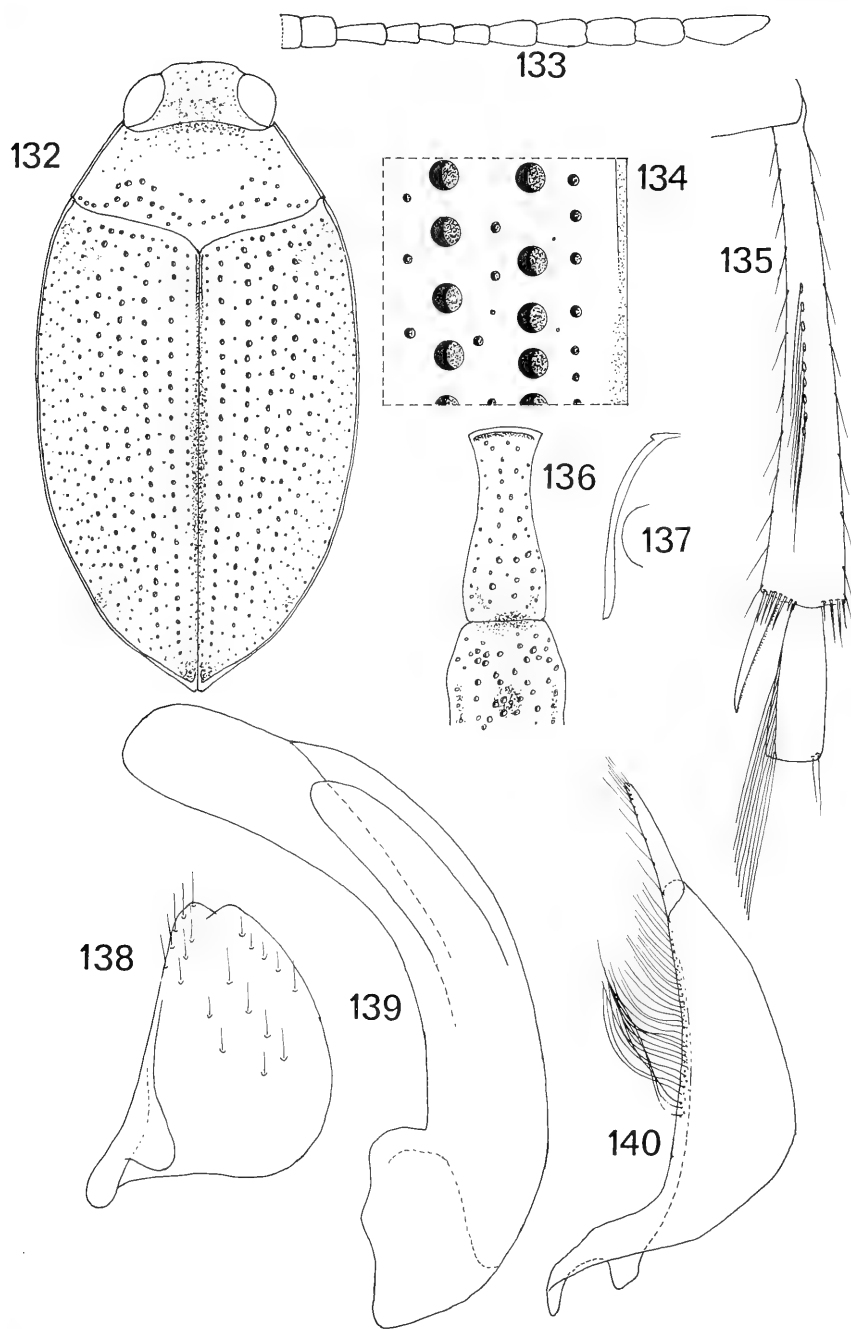
Head. – Yellow-brown, vertex brown, moderate strongly punctured, on the vertex strong darkened punctures. Distance between the eyes 1.4-1.6 × eye-width. Antennae (fig. 133) and palpi yellow to yellow-brown.

Pronotum. – Yellow to yellow-brown, anterior margin darkened in the middle. Lateral borders straight, finely bordered. Moderate strongly punctured, along the base with a partly double row of strong punctures, discal punctures brown, basal punctures black.

Elytra. – Yellow, darkened suture narrow, at most reaching the secondary punctures on the disc, vague brown blotches on the shoulders and in the apical part (fig. 132). Primary punctures strong, 28 punctures in the first row. Secondary punctures strong. All punctures darkened (fig. 134).

Ventral side. – Yellow to yellow-brown, elytral epipleura yellow, legs yellow-brown, some darkening towards the coxae. Prosternal process flat, moderate strongly punctured, narrowed near the coxae (fig. 136), lateral plicae complete (fig. 137). Metasternal process flat with a small pit in the middle, strongly and densely punctured (fig. 136). Setiferous striae $\frac{1}{3}$ × the tibia length, with about 10 punctures, longer of the two tibial spurs $\frac{3}{5}$ × the length of the first tarsal segment (fig. 135).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 138-140.



Figs. 132-140. *Haliplus gafnyi*, holotype. – 132, dorsal view; 133, antenna; 134, elytral punctuation; 135, dorsal side of hind tibia; 136, prosternal process; 137, lateral view of prosternal process; 138, left paramere; 139, penis; 140, right paramere.

Etymology. – Named after the late Mr. Gabriel Gafny, Hydrologist of the Nature Reserve Authority of Israel.

Biology

In temporary pool.

Distribution (fig. 303)

Only known from Israel.

15. *Haliplus guttatus* Aubé (figs. 141-149)

Haliplus guttatus Aubé, 1836: 27. Lectotype ♂ (here designated), unlabelled (MNHN, coll. S.E.F. Aubé) [examined].

Haliplus pelopis Sahlberg, 1907: 21. Lectotype ♂ (here designated), Elis, J. Sahlb., Spec. typ., 2284, Mus. Zool. H.fors, Spec. typ. No. 852, *Haliplus pelopis* J. Sb. [aedeagus missing] (UZMH) [examined]. Syn. n.

Haliplus guttatus; Aubé 1838: 15, Müller 1900: 113, Apfelbeck 1904: 359, Fiori 1904: 195, Escalera 1914: 57, Zimmermann 1920: 308, 1924: 135, Guignot 1928: 145, 1933: 232, 1947: 52, 1959: 36, Scholz 1929: 15, F. Burmeister 1939: 213, E. Burmeister 1987: 177, Csiki 1946: 560, Zaitsev 1953: 72, Lagar Mascaró 1968: 73, Ienistea 1978: 294, Franciscolo 1979: 122.

Haliplus pelopis; Zimmermann 1920: 314, 1924: 135, Burmeister 1939: 214, Zaitsev 1953: 72, Ienistea 1978: 294.

Diagnosis

Very variable in shape, from oval to strongly parallel, maculation not always clearly visible.

Description.

Length 3.6-4.1 mm, width 1.7-2.1 mm. Body parallel to subparallel (fig. 141).

Head. – Yellow-red to rust-coloured, dark blotch on vertex, weakly, behind the eyes more strongly punctured. Distance between the eyes 1.7-1.9 × eye-width. Antennae (fig. 142) and palpi yellow-red.

Pronotum. – Yellow to rust-coloured. Lateral borders convex to nearly straight, sometimes slightly concave before the basal corners, finely bordered. Weakly and sparsely, in the basal part densely punctured, basal row of darkened punctures twice as wide as the elytral punctures.

Elytra. – Yellow with a variable pattern of vague, sometimes hardly visible blotches, in most cases a large blotch on the suture (fig. 141). Fine primary punctures basally stronger, about 37 punctures in the first row. Secondary punctures weak. All punctures darkened (fig. 143).

Ventral side. – Body yellow to yellow-red, elytral epipleura yellow, legs yellow-red, some darkening towards the coxae. Prosternal process flat, slightly

narrowed near the coxae (fig. 145), lateral plicae complete (fig. 146), coarsely and densely punctured. Metasternal process flat with a shallow pit in the middle, weakly and sparsely punctured (fig. 145). Setiferous striole on dorsal face of hind tibia about $\frac{1}{3}$ × the tibia length with 5-10 punctures, longer of the two tibial spurs $\frac{2}{3}$ to $\frac{3}{4}$ × the length of the first tarsal segment (fig. 144). Length of hind tarsus including claws 1.3-1.4 × the tibia length, first tarsal segment about 1.3 × the length of the second segment.

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 147-149.

Biology

In stagnant water, fresh or brackish, even in brooks.

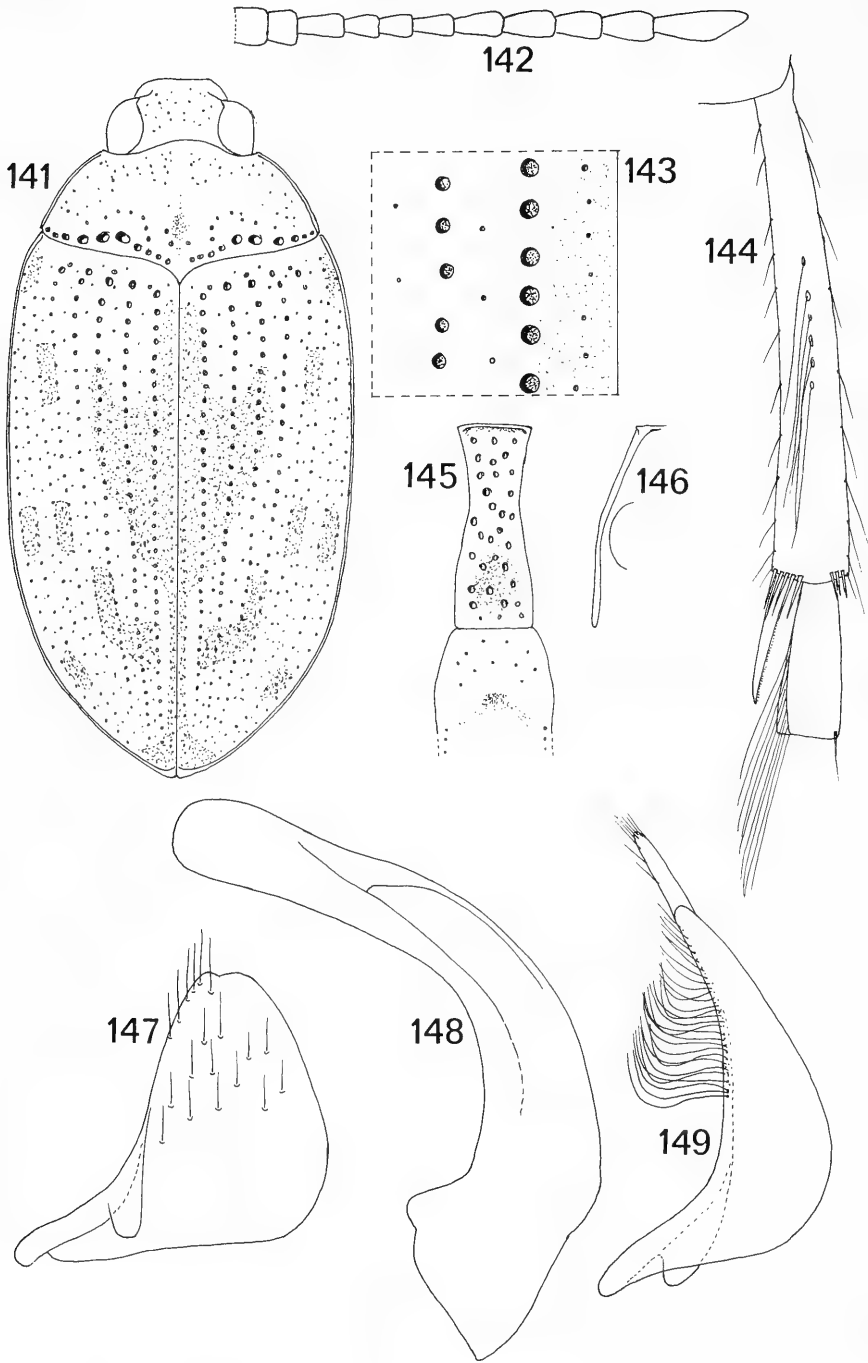
Distribution (fig. 297)

Mediterranean, south and south-west of France, Corsica, Spain including Baleares, Italy including Sardinia and Sicily, Malta, Yugoslavia, Greece, North Africa: Morocco, Algeria, Tunisia. All records from Poland and the southern states of the USSR are suspect and likely concern other species such as *fulvus*, *variegatus* or *maculatus*.

Remarks

The types of *guttatus* and *pelopis* have been examined. They do not show all differences used in earlier identification-keys. I regard both conspecific.

Material examined. – 67 ex. – Algeria: 5 ex.; 2 ex., Algiers, v.1861, H. Clark; 3 ex., Kraatz; 3 ex., lac des Serpents, Djijellé, Massif des Mouzaia (BMNH); 1 ex., Philippeville (MNHN); 2 ♀, Taguin; 4 ex., Prov. d'Alger, Taguin, 1895, de Vauloger (NHMW). – France: 1 ex., Nizza, (NHMW); 1 ex., Montpellier, v.1861, H. Clark (BMNH); 1 ex., Camargue, nr. Salin de Giraud, 12.vi.1980 (Huijbregts); 1 ex., Albaron (B. du R.), L. Schaefer (RMNH); 1 ex., Albaron (B. du R.); 1 ex., Pyrénées; 1 ex., Montfort, Landes (ZMAN); 2 ex., Beragne (MNHN); 1 ex., Les Angles, Gard. iv.1928; 1 ex., Camargue; 1 ex., Corsica, 1905, Aleria; 4 ex., Hyères (BMNH). – Greece: 1 ♂ (Lectotype of *pelopis*) (UZMH); 1 ex. (MNHN); 2 ex., Acarnan, 8.ii.1969, Forster (OLML); 1 ex., Attika (ZMAN); 4 ex., Zante, Kalamaki, 1909, M. Hilf; 1 ex., Khalkidhiki, Sithonia, 22.vii.1988, M.Jäch; 1 ex., Kérkira, Stephanides (NHMW). – Italy: 1 ex., Sardinia, Assuni, Krausse (NHMW); 1 ♂, Sardegna, Gag., 7 km W. of Carbonia, alt. 20 m., 6.v.1984 (Huijbregts); 1 ex., Lucania, Policorof M.T., 3.xi.1972, Angelini; 1 ex., Toscane, Dahl (RMNH); 1 ♂, Florenz, Brozzi (OLML); 1 ex., Etruria, (BMNH). – Malta: 1 ex., Chadwick Lakes, 31.i.1987, M. Borg, fresh water (NHMW). – Spain: 2 ex., Palencia (MNHN, ZMAN). – Yugoslavia: 1 ♂, Zadar (Zara), Sturany, 1891 (NHMW). – Locality not traced: 1 ex., S. Sparato, Dodero (MNHN)



Figs. 141-149. *Haliplus guttatus*, Zante, Greece. – 141, dorsal view; 142, antenna; 143, elytral punctuation; 144, dorsal side of hind tibia; 145, prosternal process; 146, lateral view of prosternal process; 147, left paramere; 148, penis; 149, right paramere.

– Without locality: 1 ♂, Lectotype of *guttatus*; 1 ♀, 2 ♂, Paralectotypes of *guttatus* (MNHN); 2 ex., 67-56 (BMNH); 1 ex., Ullr.; 2 ex., Dhl., aa 44 (NHMW)

16. *Haliplus holmeni* sp. n.
(figs. 150-160)

Type material: Holotype ♂, [China] 'Yunnan, Museum Paris, coll. Maurice Régimbart, 1908' (MNHN).

Diagnosis

Looks related to *sharpi*, but the male has a left paramere with a solid digitus. The fore tarsi have a cushion between the claws.

Description

Length 3.3 mm, width 1.7 mm. Body oval, widest in the middle (fig. 150).

Head. – Brown with yellow labrum, dark blotch on vertex, moderately strongly punctured, unpunctured band between the hind parts of the eyes. Distance between the eyes $1.2 \times$ eye-width. Antennae yellow, base of eighth till eleventh segment slightly darkened, top of ultimate segment pale (fig. 151), palpi yellow.

Pronotum. – Yellow-brown to brown anteriorly, lateral borders somewhat irregularly convex, brown and clearly bordered. Width at the base $2.0 \times$ the length in the middle and $1.9 \times$ the width in front. Sparsely, anteriorly densely, basally strongly punctured. Basal punctures black and partly widened. Slightly impressed along the central part of the base (fig. 150).

Elytra. – Yellow-brown with extensive black markings: wide band along the base till the fifth puncture-row, suture, arrow-shaped central blotch and blotches on the apical half, the apex and three large blotches on the fifth to ninth interval. Primary puncture-rows strong, about 24 punctures in the first row, third to fifth row close to each other in the central part. Secondary punctures moderately strong (fig. 152). Primary and secondary punctures tending to form transverse impressions in the basal part. All punctures darkened.

Ventral side. – Rust-coloured to brown, elytral epipleura yellow-brown, legs yellow-red, darkened towards the coxae. Prosternal process slightly impressed, stronger impressed apically, densely punctured, slightly narrowed near the coxae (fig. 155), lateral plicae complete (fig. 156). Metasternal process flat, impressed apically and a shallow pit in the middle, sparsely punctured (fig. 155). Coxal plates rather strongly punctured, along the suture weakly punctured, short hairs in the punctures, only few small punctures between the normal ones (fig. 157). Hind margins of the fifth and sixth abdominal sternite with complete puncture-rows (fig.

157). Setiferous striole consisting of about 6 separate punctures, longer of the two tibial spurs about $\frac{2}{3}$ the length of the first tarsal segment (fig. 154).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Between the fore-claws a small cushion (fig. 153). Penis and parameres as in figs. 158-160, left paramere with a parallel solid digitus.

Etymology. – This species is named after my colleague specialist of Haliplidae, Mogens Holmen.

Distribution (fig. 312)

Only known from south-west China (Yunnan)

17. *Haliplus jaecki* sp. n.
(fig. 161-169)

Type material: Holotype ♂, [Turkey], 'TR, Bismil ö, Diyarbakir, 29.v.1987 (35), Jäch' (NHMW).

Diagnosis

This species is related to *kulleri* and *ortali*. The left paramere has a strongly developed solid digitus and on the inner margin a well developed row of setae.

Description:

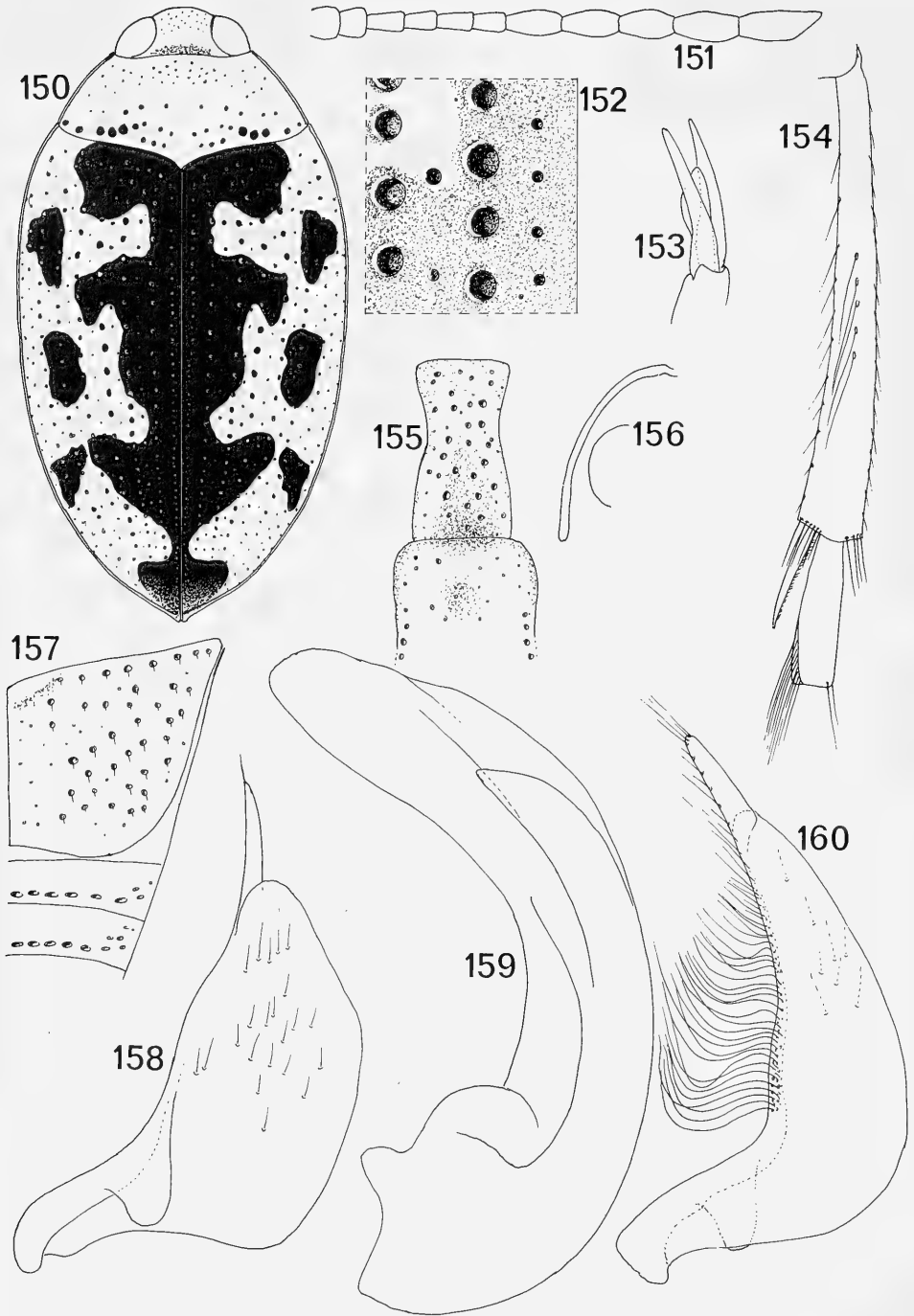
Length 3.3 mm, width 1.6 mm. Body oblong oval, widest in the middle (fig. 161).

Head. – Brown, puncturation moderately strong and dense, unpunctured band between the hind parts of the eyes. Distance between the eyes $1.4 \times$ eye-width. Antennae yellow-brown, second to fourth segment yellow, third segment $1.5 \times$ the length of the fourth segment (fig. 162). Palpi yellow-brown.

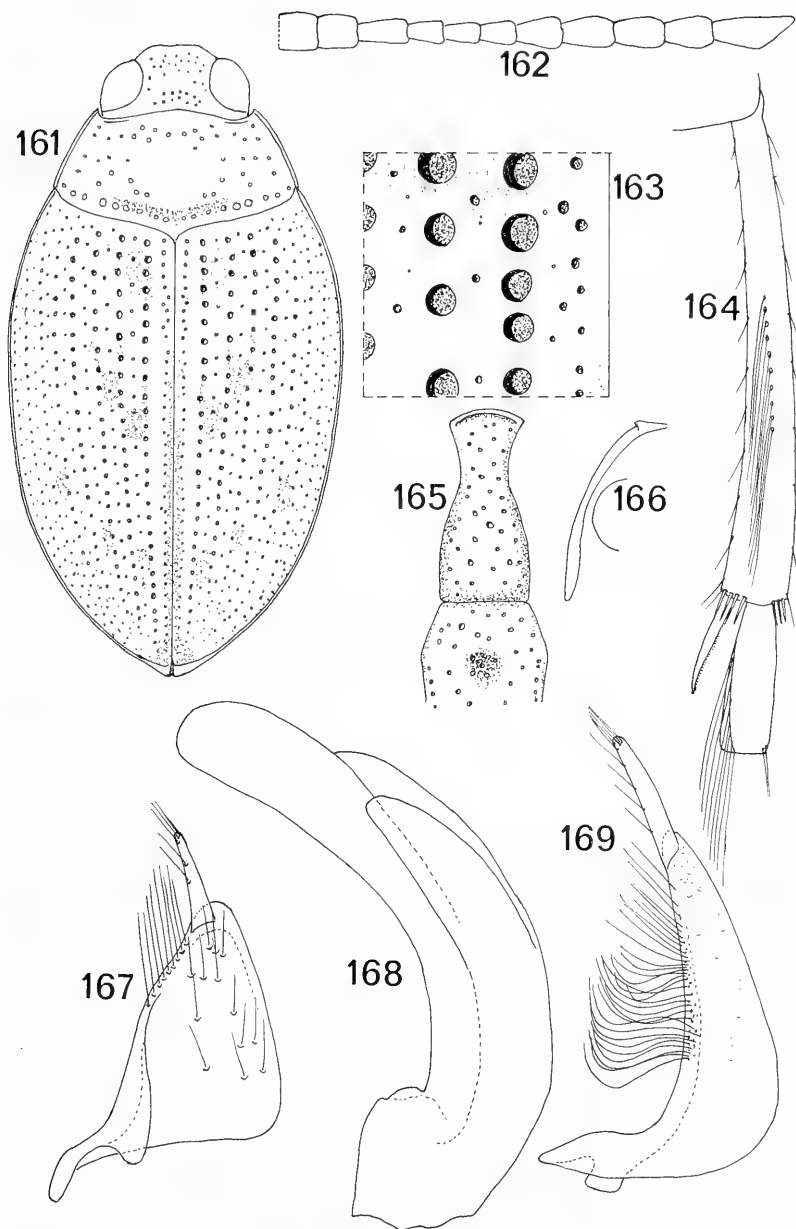
Pronotum. – Yellow-brown. Lateral borders slightly convex, darkened and clearly bordered. Width at the base $1.8 \times$ the length in the middle and $1.5 \times$ the width in front. Sparsely punctured, on the disc almost unpunctured, along the base some slightly darkened larger punctures. Along the base weakly impressed (fig. 161).

Elytra. – Yellow to yellow-brown, darkened suture and apex, vague blotches on the even intervals. Near the base a transverse slightly darkened band. Primary puncture-rows moderately strong, 28 punctures in the first row. Secondary punctures moderately strong, accompanied by very small punctures (fig. 163), all punctures darkened.

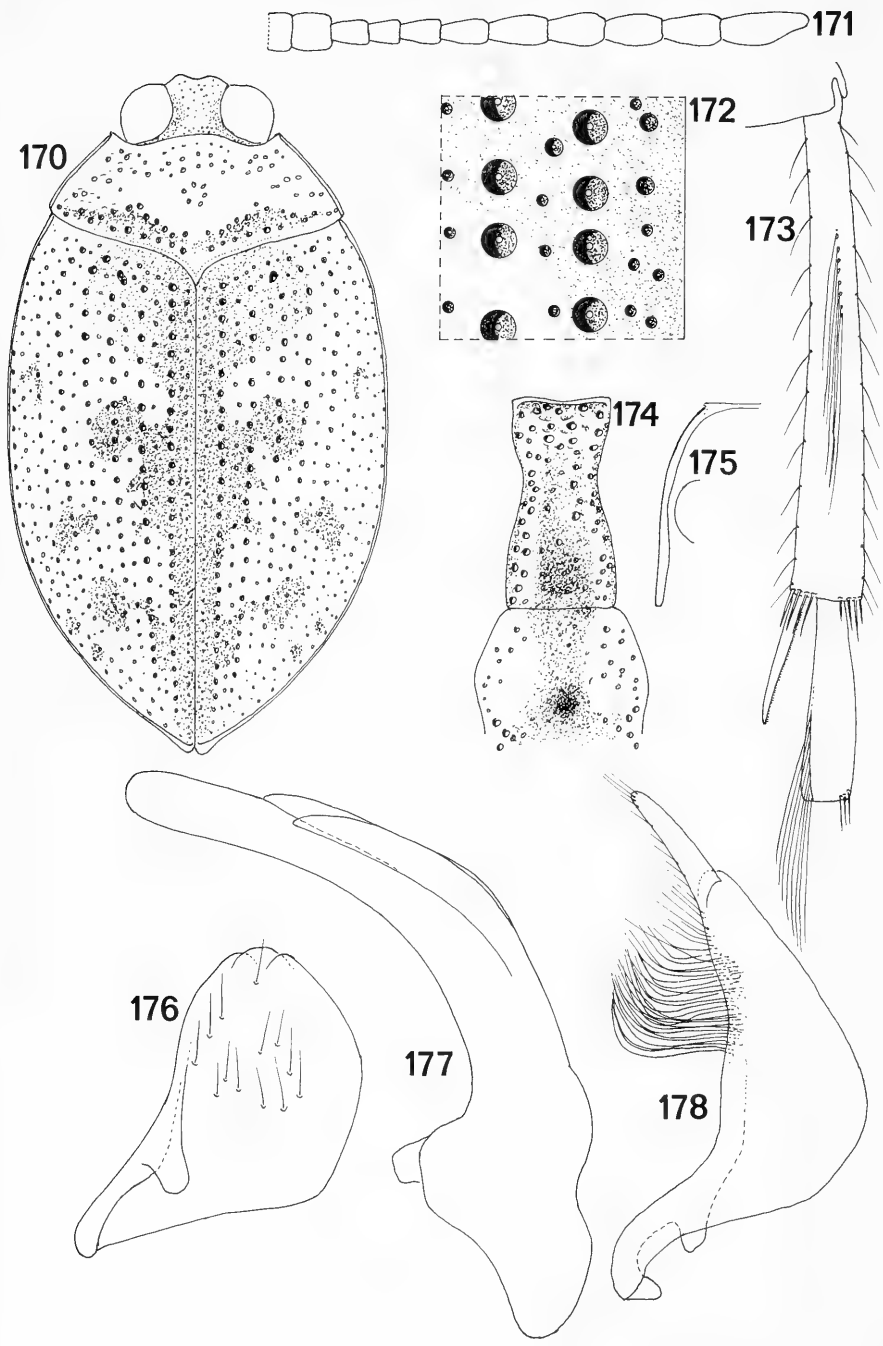
Ventral side. – Yellow to yellow-brown, elytral epipleura yellow, legs yellow-brown, darkened towards the coxae. Prosternal process slightly convex, strongly narrowed near the coxae, rather weakly punctured (fig. 165), lateral plicae complete



Figs. 150-160. *Haliplus holmeni*, holotype. – 150, dorsal view; 151, antenna; 152, elytral punctuation; 153, fore claws; 154, dorsal side of hind tibia; 155, prosternal process; 156, lateral view of prosternal process; 157, hind coxal plate; 158, left paramere; 159, penis; 160, right paramere.



Figs. 161-169. *Haliphus jaechi*, holotype. – 161, dorsal view; 162, antenna; 163, elytral punctation; 164, dorsal side of hind tibia; 165, prosternal process; 166, lateral view of prosternal process; 167, left paramere; 168, penis; 169, right paramere.



Figs. 170-178. *Haliplus kotoshonis*, Okinawa. – 170, dorsal view; 171, antenna; 172, elytral punctuation; 173, dorsal side of hind tibia; 174, prosternal process; 175, lateral view of prosternal process; 176, left paramere; 177, penis; 178, right paramere.

(fig. 166). Metasternal process flat with a shallow impression in the middle, sparsely punctured (fig. 165). Coxal plates sparsely punctured. Setiferous striae on dorsal side of hind tibia about $\frac{1}{4}$ of the tibia length, with about 7 punctures, longer of the two tibial spurs $\frac{2}{3}$ the length of the first tarsal segment (fig. 164).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 167–169, left paramere with a solid digitus and a well developed row of long bristles on the inner margin.

Etymology. – Named after the collector Dr. Manfred Jäch.

Distribution (fig. 302)

Only known from south-east Turkey, Bismil.

18. *Haliplus kotoshonis* Kano & Kamiya

(figs. 170–178)

Haliplus kotoshonis Kano & Kamiya, 1931: 2. Types burned during World War II (Nakane pers. comm.).

Haliplus kotoshonis; Sato 1984: 2, Nakane 1985a: 64, 1987: 30.

Diagnosis

This species resembles *pulchellus* and *maculipennis* by having the eyes close to each other, but it can be distinguished by the simply impressed prosternal process and the lack of a basal black elytral band.

Description

Length 3.5–3.6 mm, width 1.9–2.0 mm. Body oval, middle part subparallel, widest in the middle (fig. 170).

Head. – Brown, along the eyes dark brown. Punctuation strong and dense. Clypeus impressed in the middle. Distance between the eyes $0.8\text{--}1.0 \times$ eye-width. Antennae (fig. 171) and palpi brown-red.

Pronotum. – Brown-red. Lateral borders slightly convex, finely bordered. Hind corners protruding and strongly rounded. Punctures very strong, except on the disc dense and along the base often coarse. Base strongly impressed.

Elytra. – Yellow-brown, dark brown maculation on sutural interval and on the apex, a central blotch on the disc and small sometimes connected blotches on the other intervals. Suture slightly bordered in the basal part and at the apex. All primary punctures strong to very strong, basal punctures coarse, 32–34 punctures in the first row. Secondary punctures strong and dense. All punctures darkened and with a small yellow centre (fig. 172).

Ventral side. – Body brown, elytral epipleura yellow-brown, legs yellow-brown to brown, slightly darkened near the coxae. Prosternal process clearly impressed in the middle, narrowed near the front coxae (fig. 174), lateral plicae complete (fig. 175), strongly and partially coarsely punctured. Metasternal process impressed and with a pit in the middle, strongly punctured (fig. 174). Setiferous striae on dorsal face of hind tibia about $\frac{1}{5} \times$ the tibia length, containing about 8 punctures, longer of the two tibial spurs about $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 173).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 176–178.

Distribution (fig. 310)

Taiwan (type-locality: isle of Kotosho), Japan (Okinawa).

Remarks

Although this species seems to belong to the oriental fauna, it is treated here for practical reasons.

Material examined. – Japan: 1 ♂, 1 ♀, Kimibaru, Ohgimi V., Okinawa-Hontō, 18.viii.1989, leg. E. Matsui (in authors coll.).

19. *Haliplus kulleri* Vondel

(figs. 179–187)

Haliplus kulleri Vondel, 1988: 97. Holotype ♂, Israel, 25.3.81, Lower Galilee, Parod Res., N. Amud Basin, 35 km W. of Akko, IES 2350, Col. 1673 (NHMW) [examined].

Diagnosis

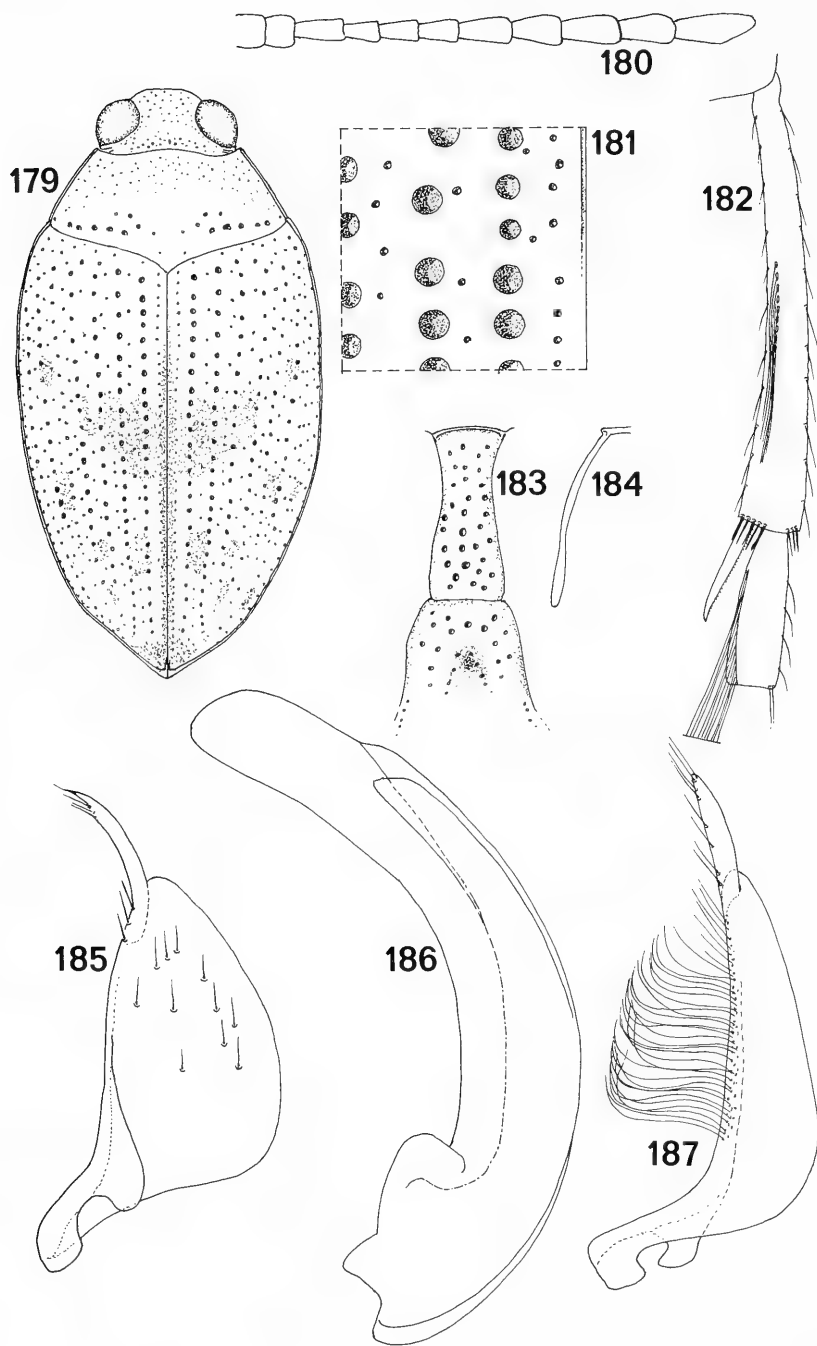
Closely related to *jaechi* and *ortali*, but in the males characterised by the long parallel-sided solid digitus on the left paramere.

Description

Length 2.9–3.0 mm, width 1.6 mm. Body fairly narrow, subparallel, widest in the middle (fig. 179).

Head. – Brown, punctuation behind the eyes rather dense, anteriorly more sparse, leaving an unpunctured shiny area between the eyes. Distance between the eyes $1.4\text{--}1.5 \times$ eye-width. Antennae (fig. 180) and palpi yellow.

Pronotum. – Yellow, slightly darkened on the disc. Lateral borders nearly straight, finely bordered. Sparsely and weakly punctured, leaving an unpunctured shiny area on the disc, two short basal rows of slightly widened and darkened punctures (fig. 179).



Figs. 179-187. *Haliplus kulleri*, holotype. – 179, dorsal view; 180, antenna; 181, elytral punctuation; 182, dorsal side of hind tibia; 183, prosternal process; 184, lateral view of prosternal process; 185, left paramere; 186, penis; 187, right paramere.

Elytra. – Yellow with a pattern of brown blotches, one triangular on the middle of the suture and some smaller ones around. Moderately strong darkened primary puncture-rows, about 30 punctures in the first row. Secondary punctures small, alternated with very fine punctures (fig. 181).

Ventral side. – Body yellow-brown, elytral epipleura yellow, legs yellow. Prosternal process slightly convex, narrowed near the coxae, covered with strong punctures (fig. 183), lateral plicae continuous (fig. 184). Metasternal process flat with a shallow pit in the middle, sparsely punctured (fig. 183). Legs half shiny, with fine micro-punctuation. Setiferous striole on dorsal face of hind tibia with about 9 punctures, longer of the two tibial spurs about $\frac{3}{4} \times$ the length of the first tarsal segment (fig. 182). Length of hind tarsus including claws $1.3 \times$ the tibia length, first tarsal segment $1.5 \times$ the length of the second segment.

Male sexual characters. – First three tarsal segments of fore- and midlegs hardly widened, scaly hairs on ventral side. Penis and parameres as in figs. 185–187, left paramere with a long parallel digitus (fig. 185).

Female: Unknown.

Biology

In temporary pool.

Distribution (fig. 302)

Only known from Israel, Lower Galilee.

Material examined: 2 ex. – Israel: 1 ♂ (holotype); 1 ♂, Berekhat Shosh, 23.i.1989, IES 5343 (HUJ).

20. *Haliplus laminatus* (Schaller)

(figs. 188–198)

Dytiscus laminatus Schaller, 1783: 314. Types not located, Schaller's material has been lost (Horn & Kahle 1936) [not examined].

Haliplus cinereus Aubé, 1836: 30. Lectotype (here designated), Gallia, 2645, coll. Chevrolat, Det. Sharp. 82, *Haliplus cinereus* Aubé p18, *affinis* Steph., Type, *cinereus* Aubé, Type d'Aubé, TYPE (pink label) (ISNB) [examined].

Haliplus laminatus ?var. *ater* Redtenbacher, 1842: 8. Types not located [not examined].

Haliplus laminatus ♀ var. *punctulatus* Penecke, 1901: 11. Types not located [not examined].

Haliplus lombardus Fiori, 1904: 198. Types not located [not examined].

Haliplus laminatus; Seidlitz 1887: 31, Apfelbeck 1904: 361, Fiori 1904: 197, Zimmermann 1920: 310, 1924: 131, Guignot 1928: 142, 1933: 229, 1947: 48, Kinel 1929: 218, Scholz 1929: 15, Balfour-Browne 1938: 12, 1940: 154, 1951: 5, 1953: 5, Burmeister 1939: 213, Horion 1941: 365, Csiki 1946: 559, Zaitsev 1953: 67, Gueorguiev 1958: 44, 1960: 23, Lindroth 1960: 42,

Lagar Mascaró 1968: 71, Freude 1971: 15, Seeger 1971a: 430, 1971b: 558, 1971c: 166, Ienistea 1974: 207, 1978: 294, Ali 1976: 92, Galewski 1976: 30, Mateleshko 1977: 68, Franciscolo 1979: 113, Fichtner 1981: 327, Holmen 1981: 2, 1987: 110, Leblanc 1984: 8, Lundberg 1986: 11, Vondel 1986: 128, 1989a: 57. *Haliplus cinereus*; Aubé 1836: 30, 1838: 18, Erichson 1837: 185, Zimmermann 1920: 310, Balfour-Browne 1936: 75, 1938: 12, Burmeister 1939: 213.

Haliplus laminatus ?var. *ater*; Zimmermann 1920: 310.

Haliplus ♀ var. *punctulatus*; Zimmermann 1920: 310.

Haliplus lombardus; Zimmermann 1920: 312, Burmeister 1939: 213.

Diagnosis

This species can be distinguished from all other palearctic species of *Liaphlus* by the dark lines on the elytral puncture-rows and in the males by the strongly dilated first mesotarsal segment and the lack of a digitus on the right paramere.

Description

Length 2.5–3.6 mm, width 1.5–1.9 mm. Body with subparallel sides in the central part (fig. 188).

Head. – Yellow-brown with brown collar, with dense and on the collar strong and darkened punctures. Distance between the eyes $2.0\text{--}2.1 \times$ eye-width. Antennae (fig. 189) and palpi yellow.

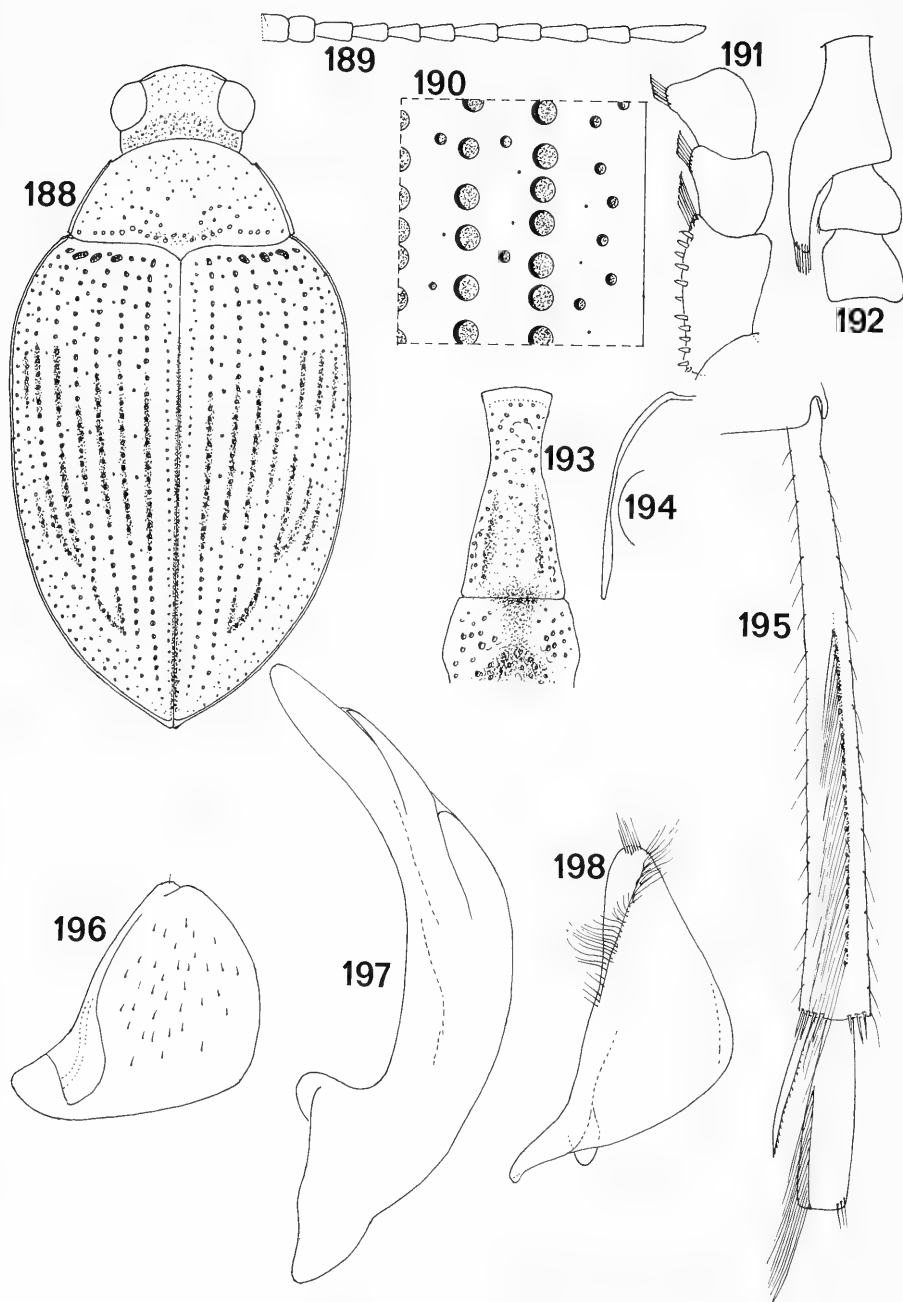
Pronotum. – Yellow. Basally not as wide as base of elytra. Lateral borders slightly convex, finely bordered. Densely, on the disc more sparsely punctured.

Elytra. – Yellow to yellow-red, strong primary puncture-rows with widened and usually groove-like basal punctures, about 42–46 punctures in the first row. Secondary punctures rather weak. All punctures darkened (fig. 190). Primary rows and suture partly, sometimes completely covered with dark lines, not connected to each other (fig. 188).

Ventral side. – Yellow to yellow-brown, elytral epipleura yellow, legs yellow to yellow-brown, coxae red-brown. Prosternal process grooved, narrowed near the coxae, widened towards the apex, punctures moderately strong and dense (fig. 193), lateral plicae complete (fig. 194). Metasternal process slightly impressed in the middle, moderately strongly punctured (fig. 193). Setiferous striole on dorsal side of hind tibia stretched over the apical $\frac{2}{3}$, longer of the two tibial spurs $\frac{3}{4} \times$ the length of the first tarsal segment (fig. 195).

Male sexual characters. – First three protarsal segments slightly widened, scaly hairs on ventral side, first segment ventrally with a complete row of strong spines (fig. 191). First mesotarsal segment strongly dilated ventrally (fig. 192). Penis and parameres as in figs. 196–198, right paramere without a digitus as characteristic for *Liaphlus* (fig. 198).

Female. – Elytra with strong micropunctuation.



Figs. 188-198. *Haliplus laminatus*, Bruges, France. – 188, dorsal view; 189, antenna; 190, elytral punctuation; 191, first tarsal segments of forelegs; 192, first tarsal segments of midlegs; 193, prosternal process; 194, lateral view of prosternal process; 195, dorsal side of hind tibia; 196, left paramere; 197, penis; 198, right paramere.

Biology

Usually in slow running water of rivers, canals and brooks, but also found in silt ponds. The adults feed on filamentous algae and invertebrates like larvae of Chironomidae and Oligochaeta (Seeger 1971b) and freshly killed *Asellus aquaticus* (Vondel 1986). The larvae (3rd and 2nd instar) were described by Vondel (1986).

Distribution (fig. 293)

Central Europe from Denmark to the east coast of Spain, central Italy and Albania and from south-east England to the European part of the USSR. The species is also recorded from Iraq (Ali 1976). The records from Ireland (Burmeister 1939, Franciscolo 1979) are doubtful.

Remarks

This species is usually treated as belonging to the subgenus *Liaphlus*, although Kinel (1929) erected a separate subgenus *Hoplites* for this species. The name *Hoplites* is preoccupied (see: International Commission on Zoological Nomenclature 1955: opinion 353), but never replaced. There is reason to believe that this species is more closely related to the subgenus *Haliplus* s. str. (Vondel 1986; Holmen 1987). Before erecting new subgeneric names it seems better to me to await the results of systematic studies on a world basis.

Material examined. – 481 ex. – Albania: 2 ex. (NHMW). – Austria: 81 ex. (ZMAN, CNCI, NHMW, NHMR). – Belgium: 2 ex. (RMNH). – Czechoslovakia: 18 ex. (ZMAN, CNCI, RMNH, MHNG, NHMW, RMNH). – France: 12 ex. (NHMW, RMNH, Jongema, BMNH, Vondel). – Germany: 20 ex. (ZMAN, NHMW, RMNH). – Great Britain: 5 ex. (BMNH). – Hungary: 3 ex. (NHMW). – Italy: 12 ex. (RMNH, NHMW). – Luxembourg: 1 ex. (ZMAN). – Netherlands: 291 ex. (ZMAN, RIN, RMNH, Cuppen, Drost, Giessen, Huijbregts, Jongema, Vallenduuk, Vondel). – Poland: 11 ex. (ZMAN, RMNH, NHMW). – Spain: 2 ex. (NHMW). – Locality not traced or unknown: 22 ex. (BMNH, NHMW, RMNH); 1 ex. (lectotype of *cinereus*) (ISNB).

21. *Haliplus maculatus* Motschulsky (figs. 199-207)

Haliplus maculatus Motschulsky, 1860: 100. Lectotype ♀ (here designated), [USSR, n.w. of Caspian sea], 'Betscho-Ko' [red label, hardly readable] '*Haliplus maculatus* Motsch., Des K. occ., 1295' [red label] (ZMUM) [examined].

Haliplus syriacus Wehncke, 1880: 73. Lectotype ♀ (here designated) 'Syria, Sharp' (MNHN) [examined]. Syn. n.

Haliplus zimmermanni Gschwendtner, 1921: 56. Lectotype ♂ (here designated) 'Oberösterreich, L. Gschwendtner, Umg. Linz, 5.5.1909, Type, Coll. Gschwendtner, *Haliplus Zimmermanni* Gs, det.

Gschwendtner, Type' [aedeagus missing] (OLML) [examined]. Syn. n.

Haliplus maculatus; Zimmermann 1920: 317, Kolosov 1931: 116, Zaitsev 1953: 75, Ienistea 1978: 294.

Haliplus syriacus; Zimmermann 1920: 317, 1924: 136, Guignot 1933: 244, Zaitsev 1953: 74, Burmeister 1985: 41.

Haliplus zimmermanni; Zimmermann 1924: 134, Müller 1926: 167, Guignot 1933: 241, Horion 1941: 365, Ienistea 1978: 295, Franciscolo 1979: 120.

Diagnosis

This species closely resembles small specimens of *fulvus*. The male can be distinguished from *fulvus* by the narrow and somewhat pointed top of the penis.

Description

Length 3.4-4.0 mm, width 1.8-2.2 mm. Body oval, widest in the middle (fig. 199).

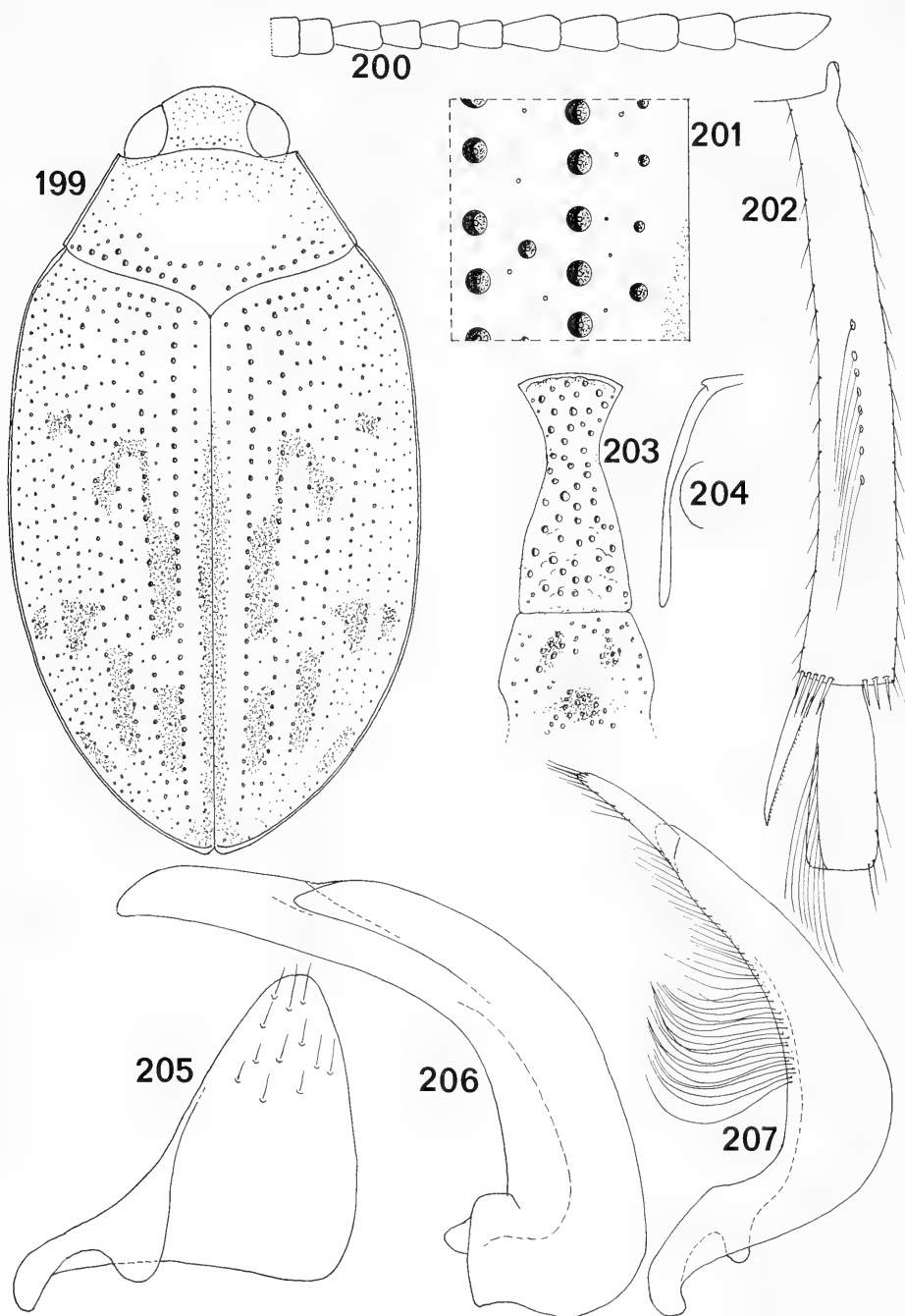
Head. – Yellow-brown to rust-coloured, vertex usually slightly darkened, weakly to moderately punctured, unpunctured band between the eyes. Distance between the eyes 1.4-1.6 × eye-width. Antennae yellow, first segment brown (fig. 200), palpi yellow.

Pronotum. – Yellow to rust-coloured. Lateral borders straight, finely bordered. Sparsely and weakly, along the base strongly punctured, basal punctures usually slightly darkened (fig. 199).

Elytra. – Yellow to rust-coloured, rather weak to moderately strong primary puncture-rows, 28-38 punctures in the first row. Secondary punctures moderately strong, accompanied by very small punctures (fig. 201), usually all punctures darkened. Markings variable, oblong blotches along the suture, on the apex and on the even intervals, the central blotches on the second and fourth interval often connected anteriorly, the markings are often hardly visible or even absent (fig. 199).

Ventral side. – Yellow-brown to rust-coloured, elytral epipleura yellow to yellow-red, legs yellow-red to rust-coloured, darkened towards the coxae. Prosternal process slightly convex, rather sparsely punctured, narrowed near the coxae (fig. 203), lateral plicae complete (fig. 204). Metasternal process flat with a shallow pit in the middle, sparsely punctured (fig. 203). Coxal plates with moderately strong and in between fine punctures, the strong punctures absent on a wide band along the suture. Setiferous striole on dorsal side of hind tibia about 1/3 of the tibia length, with 7-10 punctures, longer of the two tibial spurs about 3/4 the length of the first tarsal segment (fig. 202).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 205-207.



Figs. 199-207. *Haliplus maculatus*, Vienna, Austria. – 199, dorsal view; 200, antenna; 201, elytral punctuation; 202, dorsal side of hind tibia; 203, prosternal process; 204, lateral view of prosternal process; 205, left paramere; 206, penis; 207, right paramere.

Biology

In temporary pools, in brooks.

Distribution (fig. 300)

Austria, Hungary, Czechoslovakia, Rumania, Yugoslavia, Italy? (identification uncertain), Poland?, Israel, Syria, Afghanistan, USSR near border with Iran east of the Caspian sea and north of the Black and the Caspian sea. All European specimens I examined are from more than 60 years ago, so the species might be extinct in Europe.

Remarks

The types of *maculatus*, *syriacus* and *zimmermanni* have been compared. Although the first two are females and the important character of the pointed top of the penis cannot be checked, I consider the three conspecific.

Material examined. – 41 ex. – Afghanistan: 1 ♀, W. Afghanistan, Hari Rud, Herat, 20.vii.1949, Danish Central Asian Expedn, St. no. 4, Ex stomach of *Lobivanellus indicus*, *Haliplus fulvus*, J. Balfour-Browne det. 1964 (BMNH). – Austria: 1 ♂ (lectotype *zimmermanni*); 1 ♀, Wien, Prater, Kniz (OLML); 2 ♂, Neusiedler See; 1 ♂, Wien surr., Smolik; 2 ♀, Lavant Tal, Car (RMNH); 1 ♂, Gars, Minarz; 5 ♂, 1 ♀, Wien, Prater; 1 ♂, surr. Wien; 1 ♂, 2 ♀, Steiermarken (Styria), Kars; 1 ♂, Klosterneuburg, Pinker (NHMW). – Czechoslovakia: 1 ♂, Veseli (Moravia, surr. Ostra), Th. v. Wanka (NHMW). – Hungary: 2 ♂, Ujpest (RMNH); 1 ♂, Szekesfehervar (Szefehervar), 1928, (OLML). – Israel: 1 ♂, Berechat Sasa, 10.viii.1985, Ortal & Jäch (HUJI); 2 ♀, Jerusalem, Sauliy (MNHN). – Italy: 1 ♀, Toscana, Dahl (RMNH). – Rumania: 1 ♂, Bocs Vasovei (N-Bogsan, Banat) (RMNH). – Syria: 1 ♀ (lectotype) (MNHN). – Yugoslavia: 1 ♀, Fruska Gora (NHMW). – USSR: 1 ♀ (lectotype of *maculatus*) (ZMUM); 1 ♀, Kopet-Dagh, Germab (OLML); 2 ♀, Geok Tepe (Caucase, Guéox-Tapa), L. Mesmin (Angus); 1 ♂, Geok Tepe (Caucase, Gök Tepe), L. Mesmin (OLML). – Locality not traced: 1 ♂, Munganast, Type, 1921, coll. Gschwendtner, *Haliplus Zimmermanni* Gschw., det. L. Gschw., Paralectotype [aedeagus missing] (OLML). – Without locality: 2 ♂, (OLML); 1 ♂, Ullr. (NHMW).

22. *Haliplus maculipennis* Schaum (figs. 208-216)

Haliplus maculipennis Schaum, 1864: 107.
Haliplus maculipennis; Régimbart 1877: 354, Sahlberg 1913: 40, Zimmermann 1920: 312, 1924: 138, Guignot 1959: 37, Alfieri 1976: 38.

Diagnosis

This species can be distinguished from other palaeartic species by the distance between the eyes being about equal to eye-width and the row of dark blotches on the elytral marginal parts.

Description

Length 3.0-3.3 mm, width 1.6-1.7 mm. Body wide with subparallel sides (fig. 208).

Head. – Yellow-red with darker vertex, weakly to moderately strongly punctured. Distance between the eyes about eye-width. Antennae (fig. 209) and palpi yellow-red.

Pronotum. – Yellow-red. Lateral borders straight, strongly bordered, posterior corners usually protruding. Strong punctures along base (fig. 208).

Elytra. – Yellow-red, primary puncture-rows weak except in the basal part of the first 3 or 4 rows, basal part of third row usually impressed, about 30 punctures in the first row. Secondary punctures weak (fig. 210). Extensive elytral markings: complete suture, a basal band until the 5th puncture-row, triangular apically hooked central blotch and several smaller blotches, 8th puncture-row with a row of small blotches (fig. 208).

Ventral side. – Body yellow-red, legs yellow-red, darkened towards the coxae. Prosternal process wide, slightly narrowed near the coxae, strongly impressed towards the apex, sparsely but strongly punctured (fig. 212), lateral plicae complete (fig. 213). Metasternal process flat with a pit in the middle, weakly punctured (fig. 212). Setiferous stria about $\frac{1}{6} \times$ the tibia length, longer of the two tibial spurs about $\frac{3}{4} \times$ the length of the first tarsal segment (fig. 211).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 214-216.

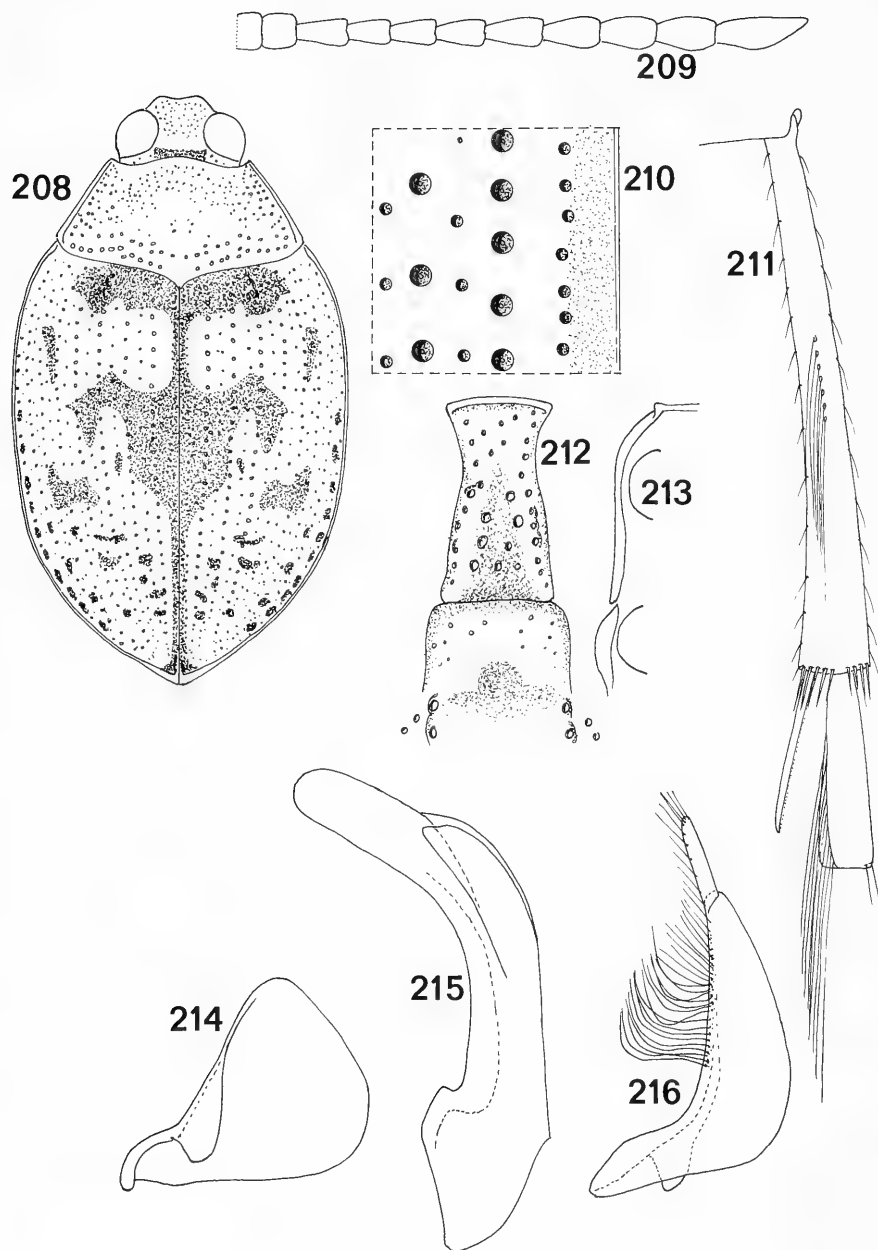
Distribution (fig. 306)

Egypt. The variety *abyssinicus* Régimbart in Egypt, Sudan, Ethiopia, Zaire, Ivory Coast and Bénin. Subspecies *capensis* Gueorguiev in South Africa.

Remarks

In the collection of München (ZSMC) 1 ♀ is present indicated as type: Egypt, Schaum, Typ, Sammlung Cl. Müller, *Haliplus maculipennis* Schaum [examined]. According to Guignot (1959) the type should be in ZMHB. [not examined]. Also because this species originates from the Ethiopian fauna I postponed the designation of a lectotype and the examination of the described varieties or subspecies until a revision of the Ethiopian fauna is undertaken.

Material examined. – 4 ex. – Egypt: 1 ♀, Schaum, Typ (ZSMC); 1 ♂, Cairo, J. Sahlb. (NHMW). – Without locality: 1 ♀, 1 ♂ (ZSMC).



Figs. 208-216. *Haliplus maculipennis* (208, 212-216, locality unknown; 209 -211, Cairo, Egypt). – 208, dorsal view; 209, antenna; 210, elytral punctuation; 211, dorsal side of hind tibia; 212, prosternal process; 213, lateral view of prosternal process; 214, left paramere; 215, penis; 216, right paramere.

23. *Haliphus mucronatus* Stephens (figs. 217-225)

Haliphus mucronatus Stephens, 1829: 40. Types probably in BMNH [not examined].

Haliphus badius Aubé, 1836: 25. Types probably in MNHN [not examined].

Haliphus parallelus Babington, 1836: 178. Types possibly in CUMZ [not examined].

Haliphus sculus Wehncke, 1883: 145. Types probably in MNHN [not examined].

Haliphus mucronatus; Schaum 1848: 42, Müller 1900: 113, Apfelbeck 1904: 359, Fiori 1904: 193, Escalera 1914: 57, Zimmermann 1920: 312, 1924: 131, Guignot 1928: 143, 1933: 229, 1947: 49, 1959: 33, Scholz 1929: 14, F. Burmeister 1939: 213, Balfour-Browne 1940: 149, 1953: 5, Horion 1941: 365, Bertrand 1949: 25, Zaitsev 1953: 67, Gueorguiev 1958: 44, 1981: 400, Lagar Mascaró 1968: 72, Freude 1971: 15, Franciscolo 1972: 65, 1979: 115, Ali 1976: 92, Ienistea 1978: 294, Fichtner 1981: 327, Leblanc 1984: 40, Vondel 1985: 33, E. Burmeister 1987: 177, Holmen 1987: 115.

Haliphus badius; Aubé 1838: 13, Schaum 1848: 42, Seidlitz 1887: 29, Zimmermann 1920: 312.

Haliphus parallelus; Schaum 1848: 42, Zimmermann 1920: 312.

Haliphus sculus; Seidlitz 1887: 29, Apfelbeck 1904: 359, Scholz 1916: 165, Zimmermann 1920: 312.

Diagnosis

This species can be distinguished from related species by the large distance between the eyes (more than $2.3 \times$ eye-width) and the metasternal process, not being grooved or pitted in the middle.

Description

Length 4.0-4.4 mm, width 1.9-2.2 mm. Body subparallel (fig. 217).

Head. – Yellow-red to brown, punctures moderately strong. Distance between the eyes $2.3-2.8 \times$ eye-width. Antennae (fig. 218) and palpi yellow-red.

Pronotum. – Yellow-red. Lateral borders slightly convex, weakly tapering anteriorly, finely bordered. Densely and fairly strongly punctured, basally with a row of widened punctures, on the disc with an unpunctured transverse band. Punctures usually darkened (fig. 217).

Elytra. – Yellow-red without markings, all primary puncture-rows about equal in strength, 45-50 punctures in the first row. Secondary puncture-rows well developed, number of punctures about the same as in the primary rows. All punctures darkened (fig. 219). Basal punctures of 3rd to 5th row usually groove-like.

Ventral side. – Body yellow to yellow-red, legs yellow to yellow-red. Prosternal process flat to slightly impressed, strongly, apically even coarsely punctured, gradually narrowed towards the coxae (fig. 221), lateral plicae complete (fig. 222). Metasternal process slightly convex, sparsely punctured

(fig. 221). Setiferous striole on dorsal side of hind tibia long, more than half of the tibia length, longer of the two tibial spurs about two thirds the length of the first tarsal segment (fig. 220).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 223-225.

Biology

In fresh or brackish water, particularly in clay and gravel pits with Characeans. The larva was described by Bertrand (1928, as *guttatus*).

Distribution (fig. 294)

Central and southern Europe: south and southeast of England, the Netherlands, Belgium, France including Corsica, Spain including Mallorca, the south of Germany, Switzerland, Italy including Sardinia and Sicily, Yugoslavia, Albania, Greece, Turkey, USSR along the Black Sea, Iraq, North Africa along the coast from Morocco till Libya. The record from the Harz mountains in East Germany was confirmed by Fichtner (1981), but he is not sure that the labelling is correct. The records from Leningrad and the Kirghiz steppes are incorrect (Zaitsev 1953).

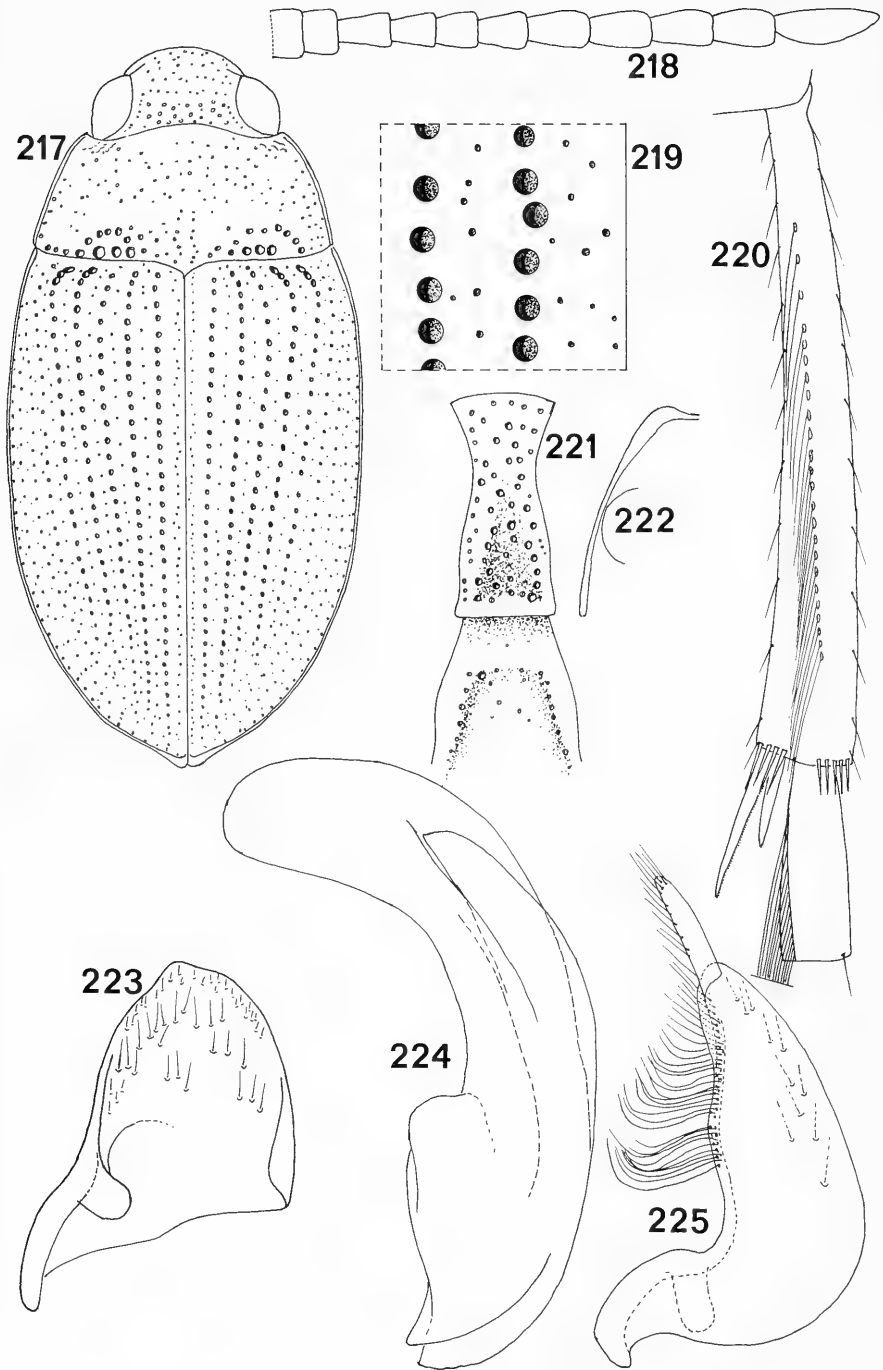
Material examined. – 116 ex. – Albania: 4 ex. (NHMW). – Algeria: 1 ex. (BMNH). – France: 26 ex. (NHMW, RMNH, Jongema, ZMAN, Vondel). – Greece: 8 ex. (NHMW, Kanaar, ZMAN). – Italy: 23 ex. (NHMW, CNCI, Jongema, ZMAN, RMNH). – Netherlands: 21 ex. (ZMAN, RMNH, Vondel). – Spain: 22 ex. (NHMW, CNCI, RMNH, ZMAN, Cuppen). – Yugoslavia: 10 ex. (NHMW, RMNH, ZMAN). – Locality not traced or unknown: 5 ex. (RMNH, NHMW).

24. *Haliphus ortalii* sp. n. (fig. 226-234)

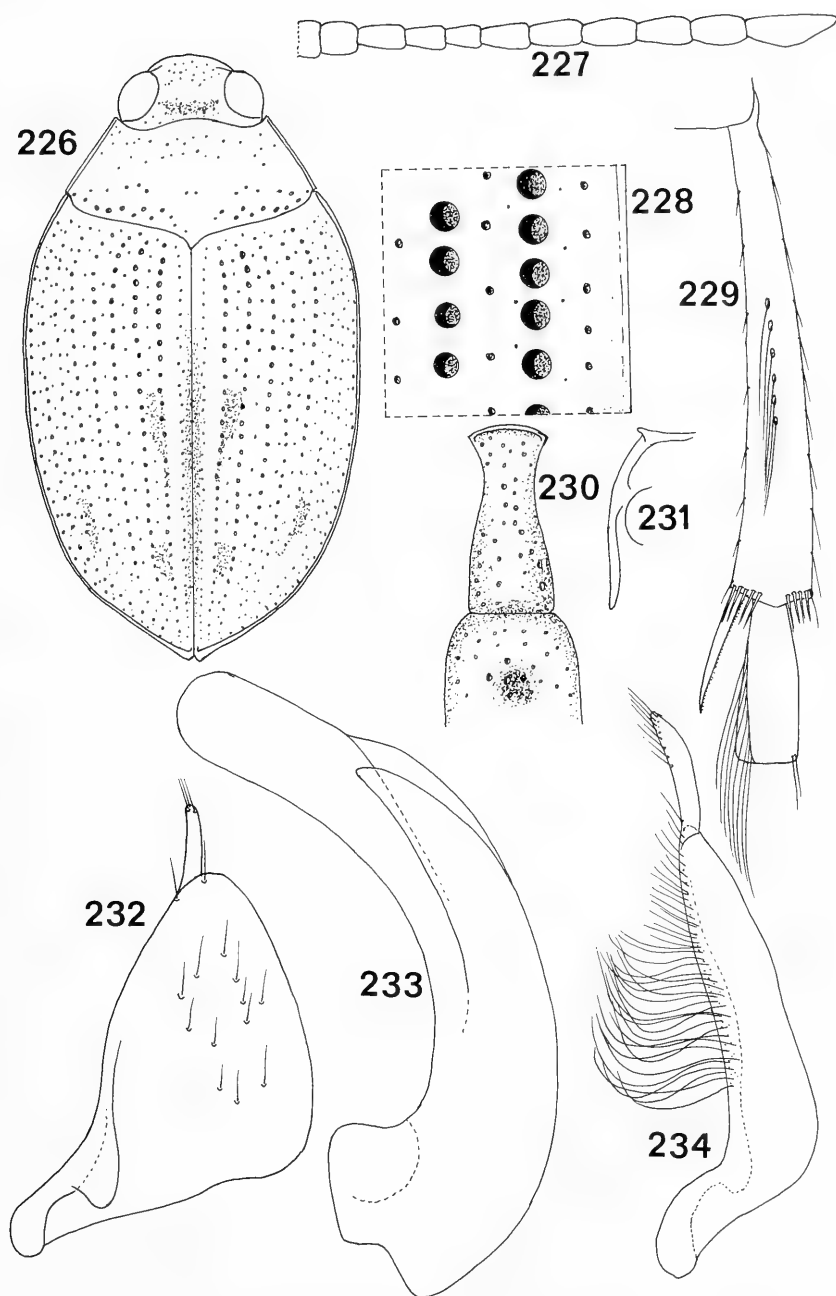
Type material: Holotype ♂, [Turkey] 'TR, Bismil ö, Diyarbakir, 29.5.1987 (35), Jäch' (NHMW). Paratypes (15 ex.): Israel: 1 ♂, 15.2.1982, Neshar quarry, rainpool, Haifa, 15.ii.1982, R. Ortal & A. Sofer, IES 2575, Col. 1751-01; 1 ♂, Neshar quarry, rainpool near Haifa, 27.i.1989, R. Ortal, IES 5344; 1 ♂, Golan, Birket sinndiane, 11.ii.1981, R. Ortal, IES 2502, Col. 2744; 1 ♀, Hula, Shosh pool, 12.i.1982, Z. Kuller & G. Gafny, IES 2599, Col. 1758; 1 ♂, 2 ♀, Berekhat, Neshar quarry, 26.xii.1989, R. Ortal, IES 5502; 1 ♂, Ein Abu Mashaq, 12.ix.1989, IES 5401 (HUJ). – Cyprus: 2 ♂, 4 ♀, Zakaki Marshes, ii.1948, G. Mavroumoustakis (Angus). – Syria: 1 ♂, Damascus, brooklet (MNHN).

Diagnosis

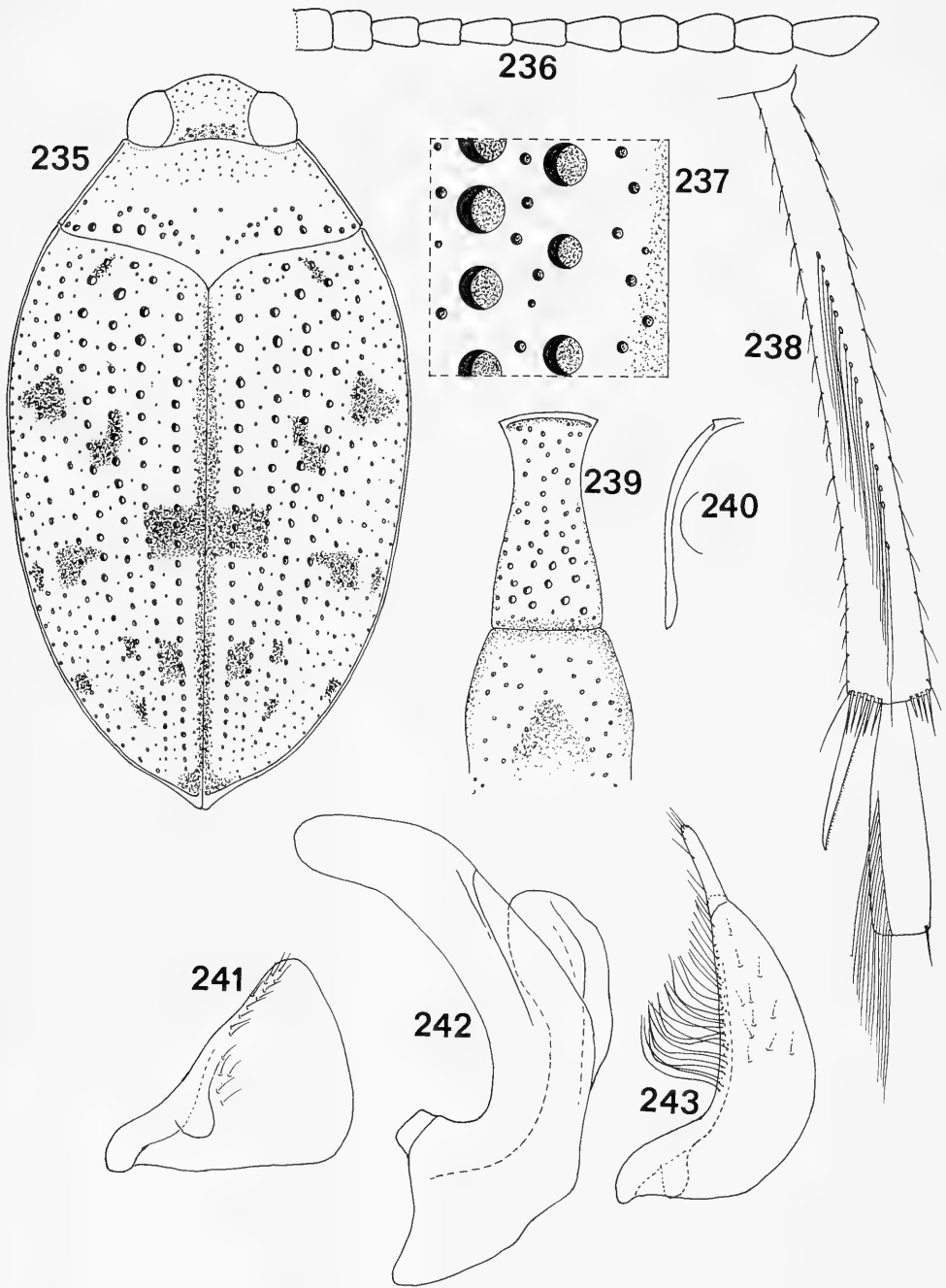
This species resembles very much species like *kulleri*, *jaechi* or even *abbreviatus*, *gafnyi* and *viliersi*. The males can be distinguished by the



Figs. 217-225. *Haliplus mucronatus*, Oostvoorne, Netherlands. – 217, dorsal view; 218, antenna; 219, elytral punctation; 220, dorsal side of hind tibia; 221, prosternal process; 222, lateral view of prosternal process; 223, left paramere; 224, penis; 225, right paramere.



Figs. 226-234. *Haliphus ortalii*, holotype. – 226, dorsal view; 227, antenna; 228, elytral punctation; 229, dorsal side of hind tibia; 230, prosternal process; 231, lateral view of prosternal process; 232, left paramere; 233, penis; 234, right paramere.



Figs. 235-243. *Haliplus ovalis*, holotype. – 235, dorsal view; 236, antenna; 237, elytral punctuation; 238, dorsal side of hind tibia; 239, prosternal process; 240, lateral view of prosternal process; 241, left paramere; 242, penis; 243, right paramere.

pointed digitus on the left paramere. In the Turkish holotype that digitus is at the top provided with 3 setae, while the Israeli paratypes have only 1 seta.

Description

Length 2.9-3.4 mm, width 1.5-1.8 mm. Body oval, widest in the middle (fig. 226).

Head. – Yellow-brown to brown, slightly darkened on the vertex, weakly punctured, unpunctured band between the hind parts of the eyes. Distance between the eyes $1.4-2.0 \times$ eye-width. Antennae yellow (fig. 227), palpi yellow.

Pronotum. – Yellow to yellow-brown on the disc, lateral borders straight, darkened and finely bordered. Width at the base $2.0 \times$ the length in the middle and $1.6 \times$ the width in front. Weakly and sparsely punctured, on the disc almost unpunctured, along the base some larger darkened punctures, along the base weakly impressed (fig. 226).

Elytra. – Yellow to yellow-brown, apical $\frac{2}{3}$ of suture darkened, clear discal blotch connected to the dark suture or vague darkening and darkened puncture-rows on the disc and vague blotches in the apical half in the even intervals. Primary puncture-rows fairly strong, about 32 punctures in the first row. Secondary punctures moderately strong, accompanied by very small punctures (fig. 228), all punctures strongly darkened.

Ventral side. – Yellow to yellow-brown, pro- and metasternal process brown, elytral epipleura yellow, legs yellow-brown, darkened towards the coxae. Prosternal process slightly convex, narrowed near the coxae, moderately strongly punctured (fig. 230), lateral plicae sometimes interrupted along the front coxae (fig. 231). Metasternal process flat with a shallow impression in the middle, sparsely punctured (fig. 230). Coxal plates rather densely punctured, small punctures between the larger ones, sutural area only weakly and sparsely punctured. Hind margins of the fifth and sixth abdominal sternite with only few punctures, coxal plates reaching the fifth sternite. Setiferous striole about $\frac{1}{5}$ of the tibia length, with about 6 coarse punctures, longer of the two tibial spurs $\frac{2}{3}$ the length of the first tarsal segment (fig. 229).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side, penis and parameres as in figs. 232-234, left paramere with a pointed solid digitus, at the top provided with 1 to 3 setae.

Etymology. – Named after Dr. R. Ortal who collected part of the type-material.

Biology

In temporary pools and in brooklet.

Distribution (fig. 303)

South-east Turkey, Cyprus, Syria and Israel,

25. *Haliplus ovalis* Sharp

(figs. 235-243)

Haliplus ovalis Sharp, 1884: 440. Lectotype ♂ (here designated), Japan, Yokohama, 29.10.81, Lewis, Type, *Haliplus ovalis* Type D. S., Sharp Coll., 1905-313' (BMNH) [examined].

Haliplus ovalis; Zimmermann 1920: 314, 1924: 134, Takizawa 1931: 141, Wu 1932: 343, J. Balfour-Browne 1946: 436, Sato 1960: 252, 1984: 3, Ohkura 1962: pl. 64, Nakane 1963: 55, 1985a: 63, 1985b: 40, 1987: 30, Cho 1969: 166, Yoon 1988: 622.

Diagnosis

This species differs from the closely related *chinensis* in having the distance between the eyes more than $1.4 \times$ the eye-width and in the male by the abruptly bent top of the penis.

Description

Length 4.1-4.3 mm, width 2.1-2.2 mm. Body oval, widest in the middle (fig. 235).

Head. – Yellow-brown, dark spot on vertex, weakly punctured. Distance between the eyes $1.5 \times$ eye-width. Antennae (fig. 236) and palpi yellow-red.

Pronotum. – Yellow, lateral borders straight, finely bordered. Densely, on the disc very sparsely punctured, basal punctures widened and darkened, sometimes only slightly.

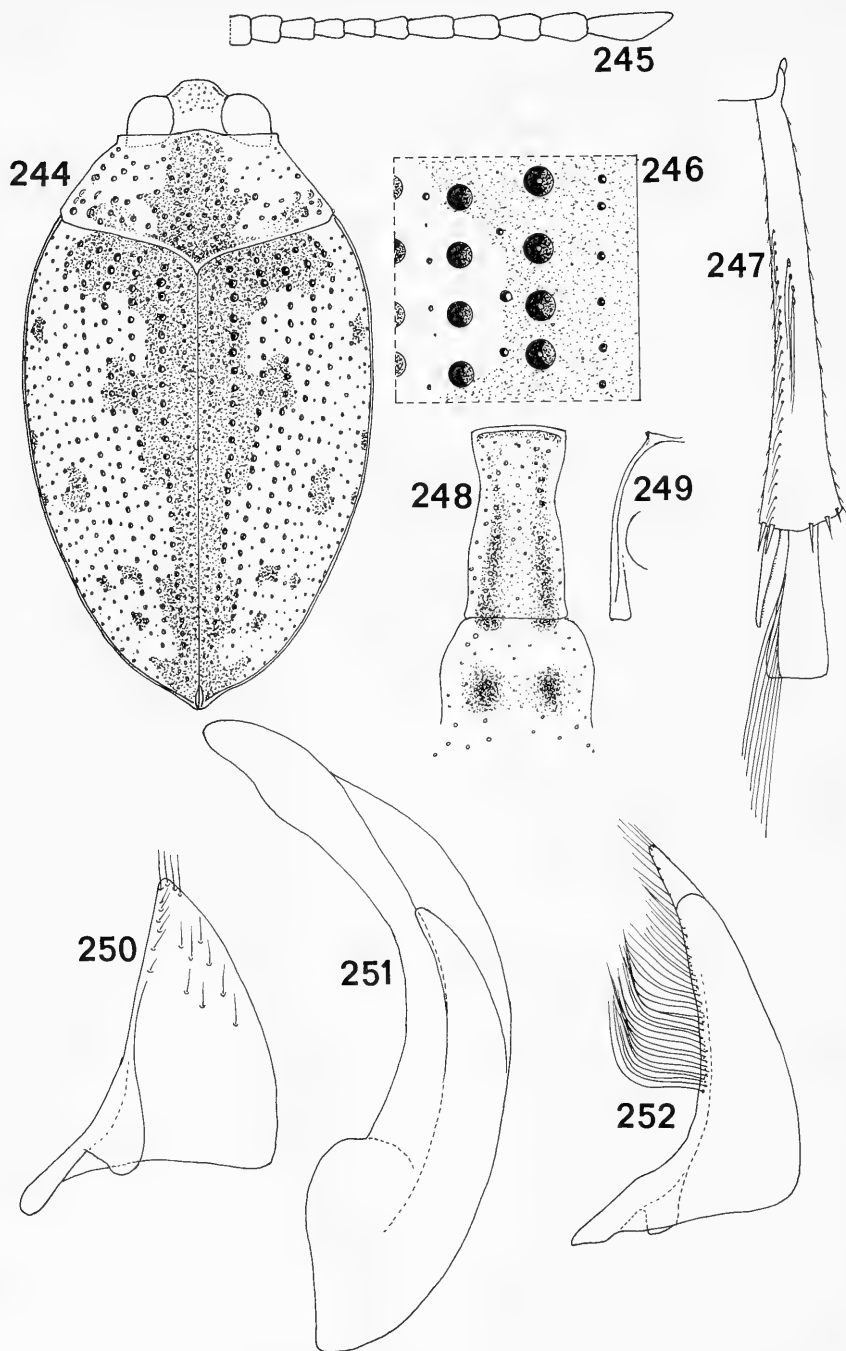
Elytra. – Yellow, moderately strong primary punctures, about 40 in the first row. Secondary punctures numerous. All punctures darkened (fig. 237). Suture, apical point and 9 or 10 spots darkened, central spots on first and third interstriae sometimes connected with suture (fig. 235).

Ventral side. – Body yellow to yellow-red, elytral epipleura yellow, legs yellow-red, gradually darkened towards the coxae. Prosternal process flat, strongly and densely punctured, narrowed near the coxae (fig. 239), lateral plicae complete (fig. 240). Metasternal process flat with a pit in the middle, rather weakly punctured (fig. 239). Setiferous striole on dorsal side of hind tibia almost half of the tibia length, with about 14 punctures, longer of the two tibial spurs two thirds the length of the first tarsal segment (fig. 238).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 241-243.

Distribution (fig. 309)

Japan: Kyushu, Honshu. The record of Korea (Takizawa 1931) probably concerns *chinensis*. The



Figs. 244-252. *Haliplus pulchellus*, lectotype. – 244, dorsal view; 245, antenna; 246, elytral punctuation; 247, dorsal side of hind tibia; 248, prosternal process; 249, lateral view of prosternal process; 250, left paramere; 251, penis; 252, right paramere.

records of China (Zaitsev 1953) likely concern *chinensis*.

Remarks

Types of the very closely related *ovalis* and *chinensis* have been examined and compared. Unfortunately the holotype of *chinensis* is a female. The shape of the penis of the lectotype and other examined Japanese specimens of *ovalis* is different from that of the continental specimens I have seen. So far I consider the Japanese specimens to belong to *ovalis* and the continental specimens to *chinensis*. J. Balfour-Browne (see Sato 1984) already noticed a difference in continental material and obviously planned to describe *Haliplus ovalis* ssp. *sinicus* from Djalantun, but that name is not known to be published and is thus unavailable.

Material examined. – 11 ex. – Japan: 1 ♂ (lectotype) (BMNH); 1 ♀, Tokio, Ahlwarth (ZMHB); 1 ♀, surr. Tokio, Bodemeyer (RMNH); 1 ♂, Murakami, Niigata Pref., 6-11.viii.1961, M. Sato; 1 ♀, Kurokawa, N-Echigo, 5.viii.1961, M. Sato (ZMUC); 1 ex., Settsu, 5.v.1931; 1 ex., surr. Tokio, E. v. Bodemeyer; 1 ex., Lewis (SMFD); 1 ex., Yokohama, 28.ix-3.xi.1881, G. Lewis (MNHN); 2 ex., Ichinokawa, Aso T., Kumamoto Pref., 28.viii.1986, E. Matsui (Vondel).

26. *Haliplus pulchellus* Clark (figs. 244-252)

Haliplus pulchellus Clark, 1863 : 418.
Haliplus oceanicus Régimbart, 1886 : 139.
Haliplus pulchellus var. *indicus* Régimbart, 1899 : 189.

Diagnosis

This species differs from other species in the area by the small distance between the eyes and the double furrowed prosternal process.

Description

Length 2.5-3.4 mm, width 1.5-2.0 mm. Body oval, widest just before the middle (fig. 244).

Head. – Brown to dark brown, darkened along the eyes and near the antennae, sometimes with a weak arrow-like darkening in the middle. Sparsely and weakly, behind the eyes more strongly punctured. Distance between the eyes $0.9-1.1 \times$ eye-width. Antennae yellow to brown-yellow (fig. 245), palpi yellow-red to brown.

Pronotum. – Yellow to yellow-red, large median dark blotch that can be reduced to a round blotch on the anterior half with a partly reduced or vague or completely absent blotch on the posterior half (fig. 244). Lateral borders straight to slightly convex, anterior corners concave, clearly, vaguely or not visibly bordered, margin never reaching the

anterior corner. Apical corners rounded, base near the scutellum usually finely impressed. Strongly, anteriorly weaker punctured, near the basal corners with one or two stronger punctures in a slight depression. Basal punctures darkened.

Elytra. – Yellow to yellow-red, clear and extended markings along the suture and along the base until the fifth primary puncture-row, a central blotch in the third interval connected to the suture and various small blotches in the lateral part (fig. 244). Primary punctures of average strength, stronger towards the base, about 30 punctures in the first row. Secondary punctures relatively strong accompanied by some very small punctures. All punctures darkened except the central hole (fig. 246). Lateral borders sometimes slightly serrulate in the basal part.

Ventral side. – Body yellow-brown to dark brown, elytral epipleura yellow to yellow-brown, legs yellow-brown with brown to dark-brown femora and coxae. Prosternal process with two strong grooves, bordered anteriorly, punctured, sometimes strongly, especially in the grooves, weakly narrowed near the coxae, slightly diverging towards the apex (fig. 248), lateral plicae complete (fig. 249). Metasternal process flat with two pits, these pits sometimes very strong and than almost forming one confluent pit, sparsely punctured (fig. 248). Coxal plates rather sparsely, near the suture weakly punctured, sutural corners more or less rectangular. Sternites with complete puncture-rows. Last sternites almost completely covered with strong punctures, apical point with a very short ridge. Setiferous striole on dorsal side of hind tibia very short, very close to the lateral row of setae and often hardly to distinguish from it, longer of the tibial spurs about $\frac{2}{3} \times$ the length of the first tarsal segment (fig. 247).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 250-252.

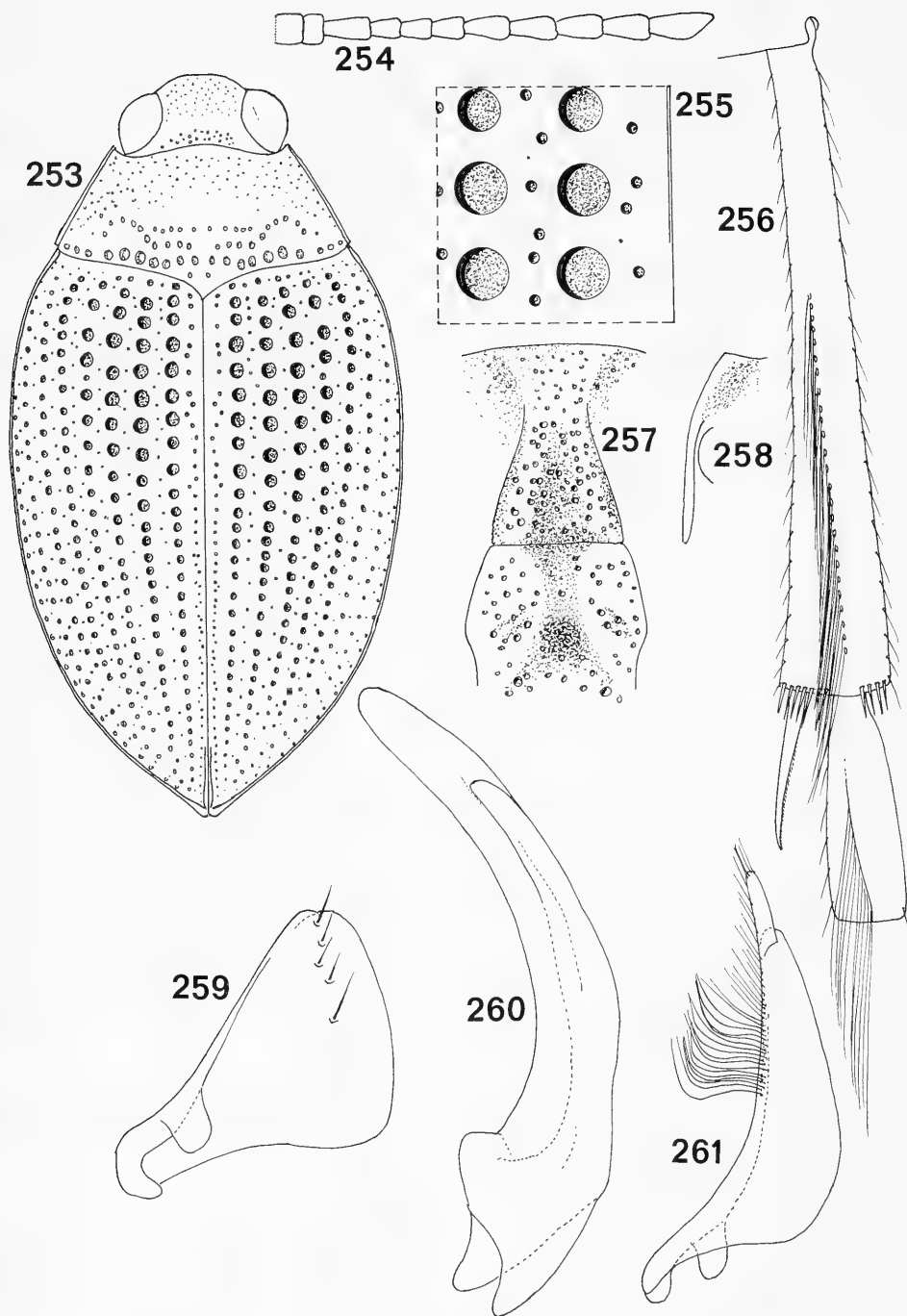
Distribution (fig. 307)

China along the coast north to Xiamen; Thailand; Vietnam; Indonesia: Sumatra, Java, Sulawesi; India; Sri Lanka.

Remarks

This species from oriental origin is included in this revision because it penetrates into China, especially along the coast. The species will be treated completely, however, in a revision of the Oriental Haliplidae.

Material examined from the treated area: 2 ex., China,



Figs. 253-261. *Haliplus rubidus*, France medit. – 253, dorsal view; 254, antenna; 255, elytral punctuation; 256, dorsal side of hind tibia; 257, prosternal process; 258, lateral view of prosternal process; 259, left paramere; 260, penis; 261, right paramere.

Amoy [Xiamen], Galatea (ZMUC). The other material will be treated in the revision of oriental Haliplidae.

27. *Haliplus rubidus* Perris

(figs. 253-261)

Haliplus rubidus Perris, 1857: 117. Types probably in Ecol. Agricult. Montpellier, France [not examined].

Haliplus perforatus Schaum, 1859: 48. Depository of types unknown [not examined].

Haliplus rubidus; Marseul 1882: 107, Seidlitz 1887: 31, Zimmermann 1920: 314, 1924: 132, Guignot 1928: 143, 1933: 230, 1947: 50, 1959: 35, Scholz 1929: 15, Burmeister 1939: 214, Lagar Mascaró 1968: 72, Ienisteia 1978: 294, Franciscolo 1979: 119.

Haliplus perforatus; Zimmermann 1920: 314.

Diagnosis

Closely related to *flavicollis*, from which it differs in the larger punctures on the elytral base, the more pronounced shoulders, the wider distance between the eyes and the usually larger size.

Description

Length 3.9-4.4 mm, width 2.0-2.3 mm. Body with strong shoulders, tapering strongly behind the middle (fig. 253).

Head. – Yellow-red to rust-coloured, weakly punctured. Distance between the eyes 1.7-1.9 × eye-width. Antennae (fig. 254) and palpi yellow-red to rust-coloured.

Pronotum. – Yellow-red to rust-coloured. Lateral borders straight, clear darkened margins, narrowed anteriorly. Densely and weakly, basally strongly punctured, some basal punctures widened (fig. 253).

Elytra. – Yellow-red to rust-coloured, very strong primary puncture-rows, near the base punctures wider than the distance from each other (fig. 255), about 30 punctures in the first row. Secondary punctures moderately strong, 20 in the second interval.

Punctures weakly darkened. No markings present.

Ventral side. – Yellow-red to rust-coloured, elytral epipleura yellow-red, legs yellow-red to rust-coloured, darkened towards the coxae. Prosternal process flat or slightly impressed and very wide apically, coarsely punctured, narrowed strongly near the coxae (fig. 257), lateral plicae absent in front of the coxae (fig. 258). Metasternal process flat, strong pit in the middle, coarsely punctured (fig. 257). Setiferous striole on dorsal side of hind tibia more than half of the tibia length, longer of the two tibial spurs little more than half the length of the first tarsal segment (fig. 256).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 259-261.

Biology

Stagnant water in pools, dune-pools.

Distribution (fig. 299)

South of France along Atlantic ocean and along the Mediterranean Sea, Italy in the province Liguria, Spain, Portugal, Morocco, Canary Islands.

Material examined. – 31 ex. – France: 1 ex., Lac d'Hourtin, Medoc, 28.ix.1973 (Jongema); 1 ex., Biarritz; 1 ex., Pyrenaei (ZMAN); 2 ex., Gallia m.; 2 ex., Gironde, Vauloger; 1 ex., France Merid, Gironde, de Vauloger; 2 ex., F. de la Teste de Vauloger (NHMW); 3 ♂, 2 ♀, Pyrenees, Biarritz; 1 ♂, 2 ♀, Sauveterre, Gard, v.1928, Guignot; 1 ex.; 1 ex., Landes; 2 ex., Pyrenees (BMNH). – Portugal: 2 ex., Alentejo prov. Rio Mira nr. S. Ana da Serra, 21.ix.1976, no. 60, 37°38'N 8°13'W, v. Berge Hengouwen (RMNH); 1 ex., Algarve, Silves, Ribeira de Arade, 10.ii.1982; 1 ex., Algarve, Porto de Lagos, barrage, 12.ii.1982 (Cuppen). – Morocco: 1 ♀, Tanger, *Haliplus fulvus* (MHNG); 1 ♂, Tanger, vii.1895 (MNHN). – Locality unknown: 1 ex. (BMNH).

28. *Haliplus sharpi* Wehncke

(figs. 262-270)

Haliplus sharpi Wehncke, 1880: 74. Lectotype ♀ (here designated), 'China, Sharp, Dr. Régimbart vidit 1898' (MNHN) [examined]

Haliplus tsukushiensis Yoshimura, 1932: 102. Depository of types unknown [not examined].

Haliplus sharpi; Sharp 1884: 440, Zimmermann 1920: 316, 1924: 137, Takizawa 1931: 142, Wu 1932: 343, Zaitsev 1953: 76, Nakane 1963: 55, 1985a: 63, 1985b: 40, 1987: 30, Sato 1984: 3.

Haliplus tsukushiensis; Ohkura 1962: pl. 64, Nakane 1963: 55, 1985b: 40, Sato 1984: 3.

Diagnosis

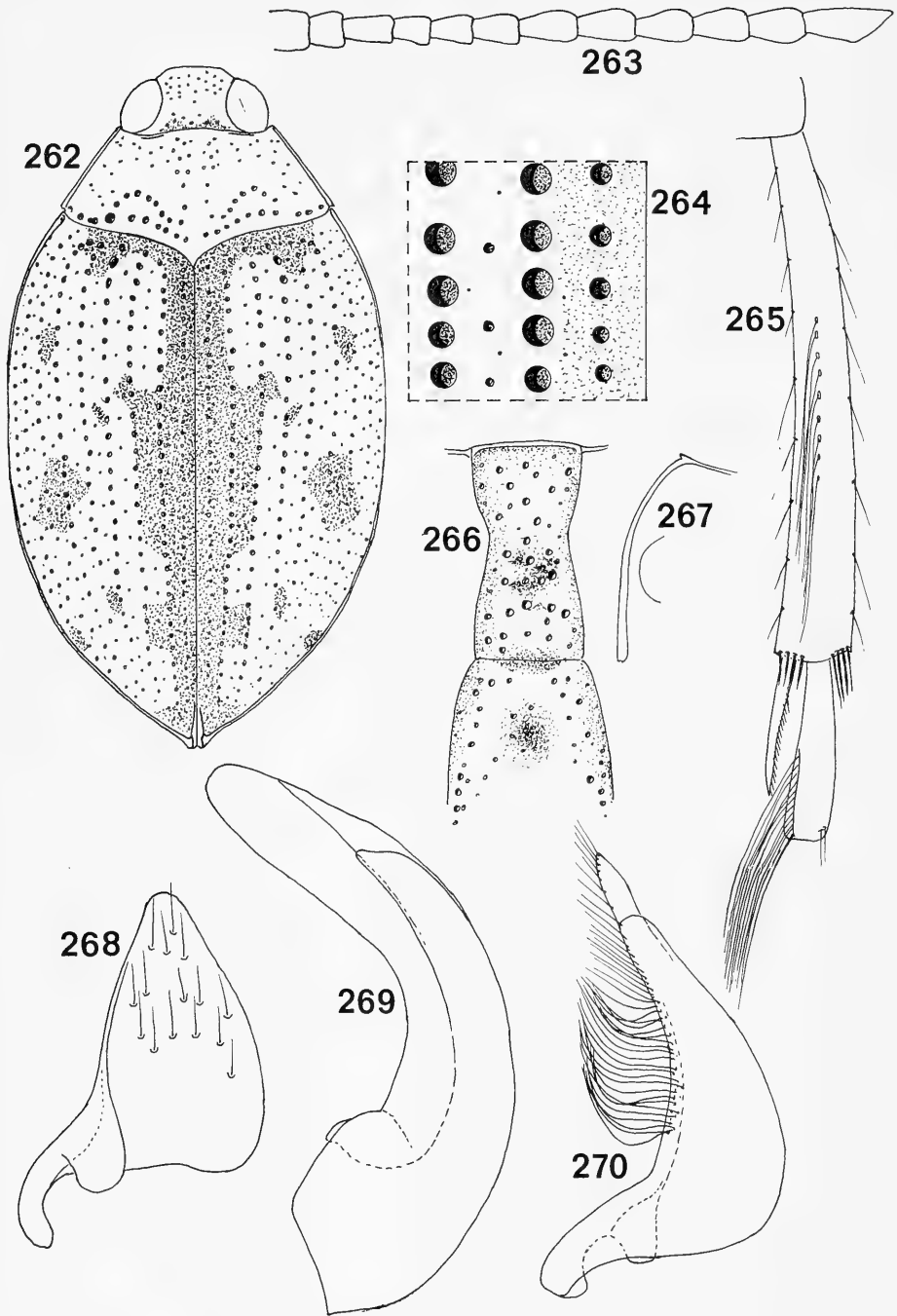
This species could be confused with specimens of *diruptus* in which a basal dark band is present on the elytra. The prosternal process in *sharpi* is wide and hardly narrowed near the coxae, while *diruptus* has a narrow prosternal process, which is strongly narrowed near the coxae. In the male the penis of both species is clearly different.

Description

Length 3.6 mm, width 1.9 mm. Body oval, widest before the middle (fig. 262).

Head. – Yellow-brown with darkened vertex and front-margin, moderately punctured. Distance between the eyes 1.3 × eye-width. Antennae yellow, first segment yellow-brown, third segment clearly longer than wide, fifth segment slightly longer than fourth (fig. 263). Palpi yellow.

Pronotum. – Yellow. Lateral borders straight, finely bordered. Sparsely, basally and anteriorly more densely punctured, on each side of the base



Figs. 262-270. *Haliplus sharpi* (262-267, lectotype; 268-270, from Korea). – 262, dorsal view; 263, antenna; 264, elytral punctuation; 265, dorsal side of hind tibia; 266, prosternal process; 267, lateral view of prosternal process; 268, left paramere; 269, penis; 270, right paramere.

with a row of partly widened and darkened punctures (fig. 262).

Elytra. – Yellow to yellow-brown, rather strong primary puncture-rows, about 36 punctures in the first row. Secondary punctures in the first interval strong and dense, in the other intervals with normal and very small punctures (fig. 264). All punctures darkened. Distinct markings along the base, suture and apical point, connected with blotches in the second interval, blotches in the fourth and sixth interval (fig. 262).

Ventral side. – Body yellow-red to brown-red, abdominal segments darkened basally, elytral epipleura yellow, legs brown-red, darkened towards the coxae. Prosternal process flat, slightly impressed in the apical part, densely punctured, slightly narrowed near the coxae, widened towards the apex (fig. 266), lateral plicae complete (fig. 267), anterior edge of prosternum strongly bordered, pro-episternum unpunctured. Metasternal process grooved and with a pit in the middle, densely punctured, basally as wide as the prosternal process (fig. 266). Coxal plates strongly punctured, width of punctures less than the distance to each other, accompanied by some very small punctures, area along the suture impressed and only weakly and sparsely punctured. Setiferous striole on dorsal side of hind tibia about $\frac{1}{3} \times$ the tibia length, longer of the two tibial spurs about $\frac{3}{4}$ of the length of the first tarsal segment (fig. 265).

Male sexual characters. – First three tarsal segments of fore- and midlegs slightly widened, scaly hairs on ventral side. Penis and parameres as in figs. 268–270.

Biology

Stagnant pools. Caught at light and in a hotel room.

Distribution (fig. 310)

China, prov. Jiangsu; Japan, Hokkaido and Shikoku; Korea.

Material examined. – 8 ex. – China: 1 ♀ (lectotype) (MNHN ex coll. Wehncke); 1 ex., Jiangsu, Shanghai, summer 1943, Marist Brothers (ISNB). – Japan: 1 ♀, 'Japon, Heller, Dr. Régimbart vidit 1898, ♀ *Haliplus sharpi* Wehncke, 1880 (paralectotype) (MNHN ex coll. Wehncke); 1 ex., Shikoku, Matsuyama, vii.1959, Light trap, (ZMUC). – Korea: 2♂, 1 ♀, Sariwon, 12–22.vii.1956, M. Magyar, (ISNB); 1 ♀, Prov. South Pyongan, Pyongyang, room of Hotel Te-dong, 30.vii.1975, J. Papp and A. Vojnits (NCI); 1 ♂, 1 ♀, Kyongpuk-do, Yongpung-kun, Hwayon-pond, 2.viii.1988, Sung Hwa Lee (Vondel).

29. *Haliplus variegatus* Sturm (figs. 271–282)

Haliplus variegatus Sturm, 1834: 157. Syntypes probably lost [as most Sturm-types] [not examined].

Haliplus subnubilus Babington, 1836: 177. Syntypes not located [not examined].

Haliplus variegatus var. *obsoletus* Westhoff, 1881: 43. Syntypes not located [not examined].

Haliplus variegatus ab. *pallidior* Müller, 1900: 115. Lectotype ♂ (here designated) [Yugoslavia] 'Castelnuovo, Humler, TYPUS, Museo Civico di Trieste, *H. variegatus* ab. *pallidior* M.' (MSNT) [examined].

Haliplus pantherinus Sahlberg, 1900? (preoccupied).

Haliplus leopardinus Sahlberg, 1900: 183 (replacement name for *H. pantherinus*). Lectotype ♂ (here designated) [Greece, Kérkira] 'Corfu, J. Sahlb., *Haliplus pantherinus* Sahlb. Type, Collect. Hauser, v. *leopardinus* det. Ganglbauer' (NHMW) [examined].

Haliplus transvolgensis Semenov, 1904: 216. Lectotype ♀ (here designated) [USSR] 'Nicolajevskij-Gorodok, Saratov, 431.V.[19]00, Sacharov, *Haliplus transvolgensis* mTyp., A. Seminov det. (ZMAS) [examined]. Syn. n.

Haliplus variegatus subsp. *galilea* Sahlberg, 1913: 40. Types not located [not examined].

Haliplus variegatus; Aubé 1836: 28, 1838: 16, Erichson 1837: 184, Schaum 1848: 42, Thomson 1854: 485, Régimbart 1877: 354, Westhoff 1881: 43, Seidlitz 1887: 30, Müller 1900: 114, Apfelbeck 1904: 360, Fiori 1904: 196, Sahlberg 1913: 39, Zimmermann 1920: 317, 1924: 136, Guignot 1928: 145, 1933: 231, 1947: 51, Scholz 1929: 17, F. Burmeister 1939: 214, Balfour-Browne 1940: 152, 1953: 5, Horion 1941: 366, Csiki 1946: 560, Zaitsev 1953: 73, Gueorguiev 1958: 44, 1960: 23, 1981: 401, Lindroth 1960: 46, Lagar Mascaró 1968: 73, Freude 1971: 15, Franciscolo 1972: 60, 1979: 121, Hosseinie 1974: 241, 1978: 167, Ienistea 1974: 208, 1978: 295, Ali 1976: 92, Galewski 1976: 29, Mateleshko 1977: 68, Fichtner 1981: 328, Holmen 1981: 2, 1987: 116, E. Burmeister 1982: 94, 1987: 184, Leblanc 1984: 8, Vondel 1985: 33, 1989a: 58, Lundberg 1986: 11, Zakharenko & Moroz 1988: 283, Nilsson 1988: 6. *Haliplus subnubilus*; Schaum 1848: 42, Zimmermann 1920: 317.

Haliplus variegatus var. *obsoletus*; Guignot 1933: 244, Zaitsev 1953: 73, Gueorguiev 1960: 23.

Haliplus variegatus ab. *pallidior*; Zimmermann 1920: 317, Scholz 1929: 17, Guignot 1933: 244, Zaitsev 1953: 74, Gueorguiev 1958: 44, 1960: 23, 1963: 216, Ienistea 1978: 295, Leblanc 1984: 8.

Haliplus leopardinus; Apfelbeck 1904: 360, Sahlberg 1913: 39, Zimmermann 1920: 317, Döbler 1976: 182.

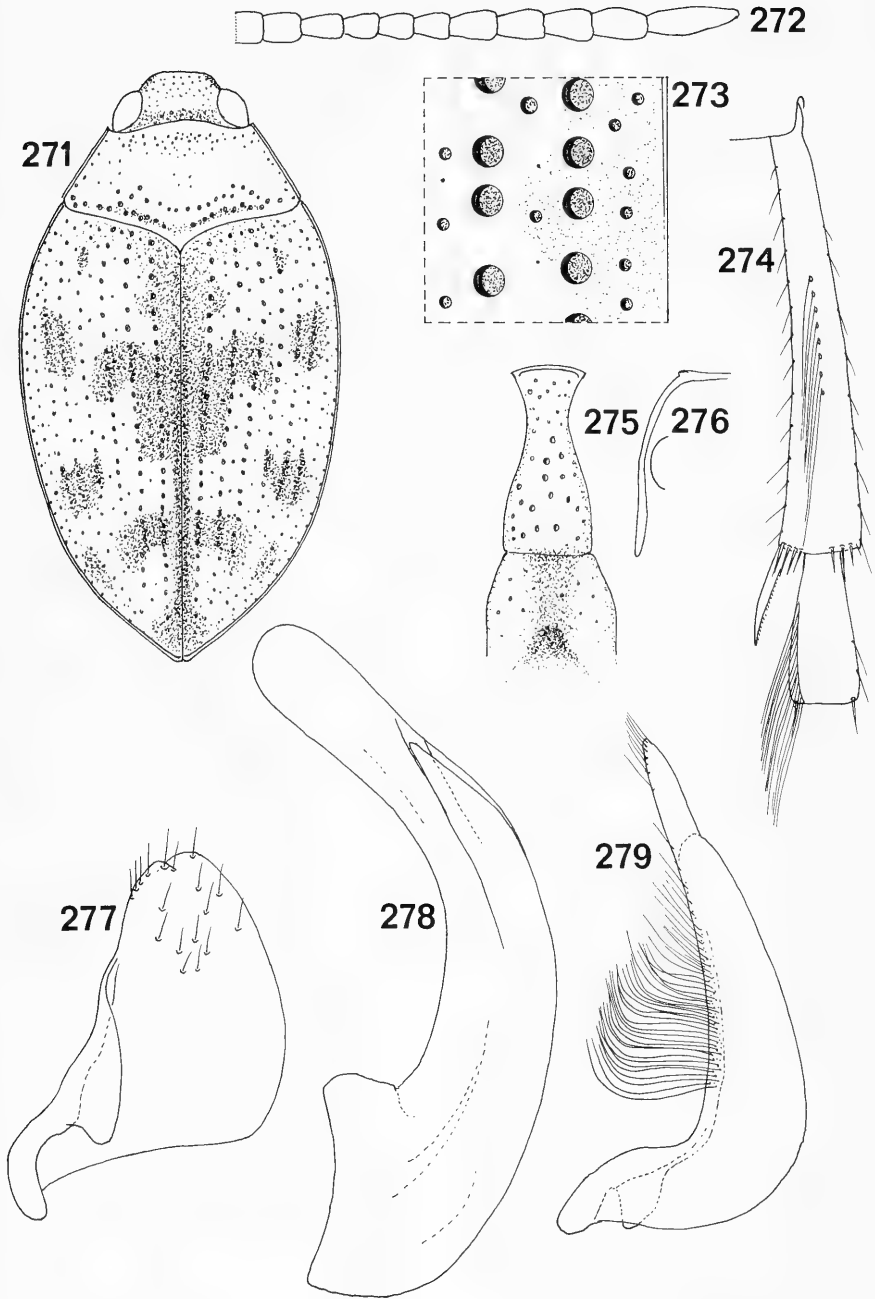
Haliplus transvolgensis; Zaitsev 1905: 37, Zimmermann 1920: 316 1924: 135, Kinel 1929: 219, Scholz 1929: 18, Burmeister 1939: 214, Csiki 1946: 559.

Diagnosis

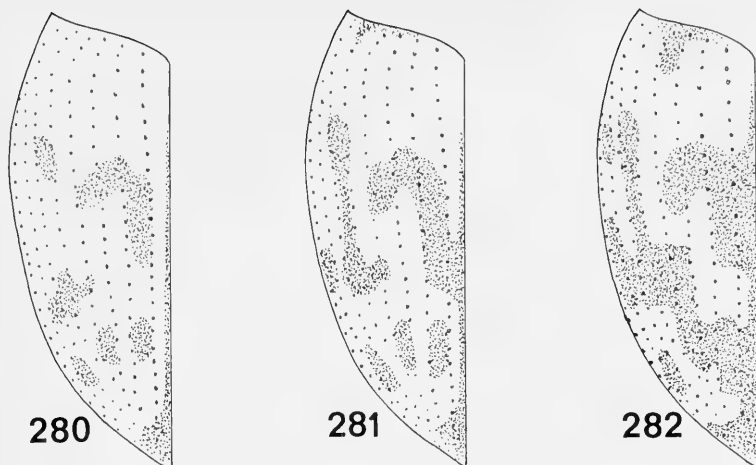
A very variable species in size, colour and maculation. The distance between the eyes, 1.7–2.0 × eye-width, usually distinguishes it from related species of the same size, especially in the Middle-East.

Description

Length 2.6–3.4 mm, width 1.4–1.8 mm. Body oval, widest before the middle (fig. 271).



Figs. 271-279. *Haliphus variegatus*, Texel, Netherlands. – 271, dorsal view; 272, antenna; 273, elytral punctuation; 274, dorsal side of hind tibia; 275, prosternal process; 276, lateral view of prosternal process; 277, left paramere; 278, penis; 279, right paramere.



Figs. 280-282. *Haliphus variegatus*, elytra. – 280, lectotype of *H. variegatus* var. *pallidior*; 281, from Castelnuovo, Yugoslavia; 282, from Trenton, England.

Head. – Yellow to rust-coloured, darkened vertex, rather weakly punctured, on the vertex with stronger darkened punctures, between the eyes with an unpunctured band. Distance between the eyes $1.7-2.0 \times$ eye-width. Antennae yellow to yellow-brown, third segment longer than the fourth or fifth segment (fig. 272), palpi yellow to rust-coloured.

Pronotum. – Yellow to rust-coloured, sometimes anterior and basal margins slightly darkened. Lateral borders straight, finely bordered. Sparsely, on the disc almost not, basally strongly punctured, basal punctures darkened (fig. 271).

Elytra. – Yellow to rust-coloured, rather strong primary puncture-rows, 26-32 punctures in the first row. Secondary punctures in the first interval fairly strong, in the remaining intervals moderately strong, accompanied by very small punctures. All punctures darkened (fig. 273). Extensive markings on the disc, along the suture, on the apex and on the even intervals with extensions to the odd intervals. The central blotches are not always connected to the suture (figs. 271, 280-282).

Ventral side. – Yellow-red to rust-coloured, elytral epipleura yellow, legs yellow-red to rust-coloured, darkened towards the coxae. Prosternal process flat or slightly convex, narrowed near the coxae (fig. 275), lateral plicae complete (fig. 276), rather coarsely punctured. Metasternal process slightly to strongly and widely grooved, coarsely punctured (fig. 275). Coxal plates sparsely, laterally more densely punctured, with a few very small punctures, apical point broadly rounded. Setiferous striole about $\frac{1}{4}$ of the tibia length, with about 5 punctures, longer of the two tibial spurs $\frac{2}{3}$ the length of the first tarsal segment (fig. 274). Hind tibia about $3 \times$ as long as the first tarsal segment.

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 277-279.

Biology

In stagnant waterbodies with fresh water with often a vegetation of Characeans, *Sphagnum* or *Hypnum*, in temporary dune-pools, in peat bogs. The third-stage larva was first described by Schiødte (1864).

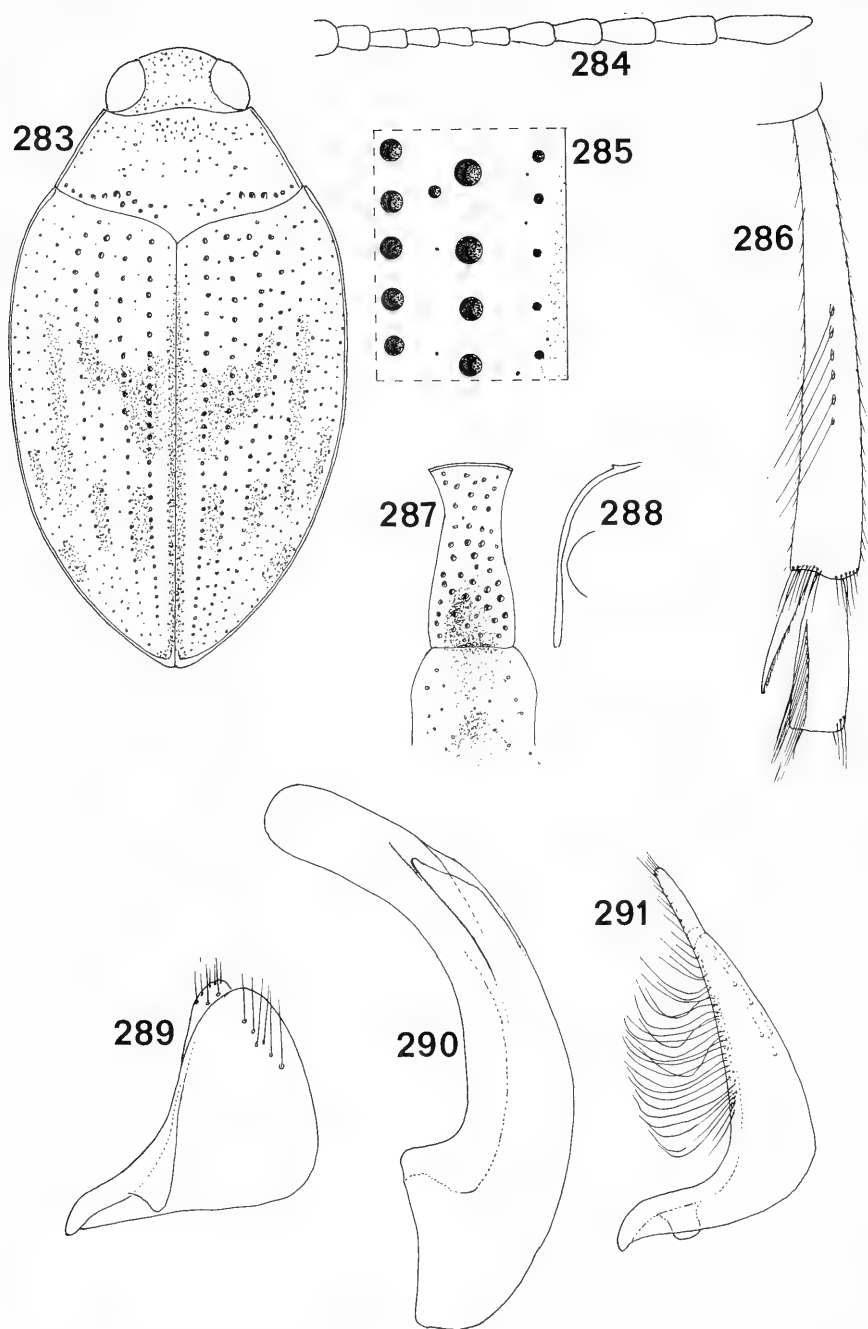
Distribution (fig. 296)

Europe: From Ireland and England to the central and southern part of European USSR, northwards to the south of Norway, Sweden and Finland and southwards to Spain, Italy and Greece. Algeria, Israel, Turkey, Syria. The records from Iraq (Ali 1976), Iran (Hosseini 1974, 1978) and Afghanistan (Gueorguiev 1963) most likely concern other species like *abbreviatus* or *villiersi*. The record from West Siberia (Zaitsev 1905, as *transvolgensis*) probably concerns *H. maculatus* or *angusi*.

Remarks

Examination of the type of *transvolgensis* showed that it is conspecific with *variegatus*. In the Mediterranean area small specimens are present, described as *pallidior* or *leopardinus*, but in my opinion these are conspecific with *variegatus*.

Material examined. – 425 ex. – Algeria: 2 ex. (BMNH). – Austria: 49 ex. (ZMAN, RMNH, NHMW, RMNH). – Belgium: 1 ex. (NHMW). – Denmark: 2 ex. (BMNH, ZMAN). – England: 31 ex. (BMNH, ZMAN, RMNH). – France: 69 ex. (MNHN, ZMAN, RMNH, NHMW, Huijbregts, Vondel). – Germany: 25 ex. (ZMAN, RMNH, NHMW, BMNH). – Greece: 1 ♂ (lectotype *leopardinus*) (NHMW), 9 ex. (paralectotypes



Figs. 283-291. *Haliphus villiersi* (283-288, holotype; 289-291, from type-locality). – 283, dorsal view; 284, antenna; 285, elytral punctuation; 286, dorsal side of hind tibia; 287, prosternal process; 288, lateral view of prosternal process; 289, left paramere; 290, penis; 291, right paramere.

leopardinus) (2 ♂, 3 ♀ NHMW; 1 ♀ UZMH; 1 ex. OLML; 1 ♂, 1 ♀ ZSMC); 38 ex. (BMNH, ZMAN, NHMW, RMNH, Huijbregts). – Hungary: 7 ex. (ZMAN, NHMW). – Ireland: 3 ex. (BMNH). – Israel: 2 ♂, Berekhat Zemorot nr. Ashkelon, 15.i.1981 (NHMW). – Italy: 15 ex. (BMNH, CNCI, NHMW, Huijbregts, Jongema). – Netherlands: 108 ex (RMNH, Schilthuizen, Cuppen, ZMAN, BMNH). – Poland: 6 ex. (BMNH, ZMAN). – Spain: 4 ex. (ZMAN, NHMW). – Sweden: 2 ex. (BMNH). – Switzerland: 1 ex. (BMNH). – Turkey: 1 ♀ (MNHN). – USSR: 1 ♀, (lectotype *transvolgensis*) (ZMAS). – Yugoslavia: 8 ex. (lectotype and 4 paralectotypes of *pallidior*) (MSNT); 10 ex. (NHMW, CNCI). – Locality not traced or unknown: 30 ex. (BMNH, ZMAN, MHNG, RMNH, NHMW).

30. *Haliplus villiersi* Legros (figs. 283–291)

Haliplus villiersi Legros, 1972: 573: Holotype ♂, 'Iran, Zabol, IV.1965, Museum Paris, Mission Franco-Iranienne 1965, A, Type, *Haliplus* (*Liaphlus*) *villiersi* n. sp., C. Legros det.' (MNHN) [examined].

Diagnosis

A variable species, that is closely related to *abbreviatus* and *variegatus*, from which it can be distinguished by the usually impressed prosternal process. Maybe *abbreviatus* and *villiersi* are conspecific.

Description

Length 3.0–3.4 mm, width 1.7–2.0 mm. Body oval, sides subparallel, shoulders a little pronounced (fig. 283).

Head. – Yellow-brown, weakly punctured. Distance between the eyes about 1.6 × eye-width. Antennae (fig. 284) and palpi yellow..

Pronotum. – Yellow-red, lateral borders straight, narrowed anteriorly, finely bordered. Weakly, along the base more strongly, on the disc more sparsely punctured, basal punctures slightly darkened (fig. 283).

Elytra. – Yellow to yellow-brown, rather weak to moderately strong primary puncture-rows, 30 to 35 punctures in the first row. Punctures of 8th and 9th row with long hairs. Secondary punctures in two types: moderately strong or very weak (fig. 285). All punctures darkened. Usually brown markings on the suture, apex, even intervals and sometimes in the first interval (fig. 283), the markings can be very weak.

Ventral side. – Body yellow to yellow-red, elytral epipleura yellow, legs yellow-red. Prosternal process flat or slightly impressed apically, coarsely punctured, slightly narrowed near the coxae (fig. 287), lateral plicae complete (fig. 288). Metasternal process flat or grooved in the middle and with a central pit (fig. 287), weakly punctured. Setiferous

striole on dorsal side of hind tibial about one third of the tibia length, longer of the two tibial spurs $\frac{3}{4}$ × the length of the first tarsal segment (fig. 286).

Male sexual characters. – First three tarsal segments of fore- and midlegs widened, scaly hairs on ventral side. Penis and parameres as in figs. 289–291.

Distribution (fig. 305)

Iran.

Material examined. – 6 ex. – Iran: 1 ♂ (holotype); 1 ♂, 4 ♀, Zabol, 19.iv.1965, Mission Franco-Iranienne 1965 (1 ♀ allotype) (MNHN)

Unnamed material

The specimens I failed to determine are listed below. Some of them might belong to still undescribed species.

Species near *H. diruptus*. – [China] 'Yunnan Fou, Yunnan, R. Mouchamps det. 63, *Haliplus diruptus* B.Br.' (1 ♀, 1 ♂ without aedeagus) (ISNB). Belonging to *Haliplus diruptus* or *H. davidi* or to an undescribed species. – [China, Beijing] 'Peping, Collector C. F. Wu, Col. Gschwendtner, *simplex* Clark Gschwendtner' (2♀) (OLML). Possibly belonging to *H. diruptus* or *H. davidi*. – [China] 'Yunnan Fou, Yunnan, H. Perrot; ♀ (MNHN). Possibly belonging to *H. diruptus* or *H. davidi*.

Species near *H. variegatus*. – [USSR] 'Ross. O.' (2 ♀) (BMNH). Possibly belonging to an undescribed species.

Species near *H. ortalii*. – [Iran] 'Perse, Susa, iv.1899, Escalera, *Haliplus* sp.x., Dr. Régimbart vidiit 1900 (1 ♀) (MNHN). Possibly belonging to *H. ortalii*.

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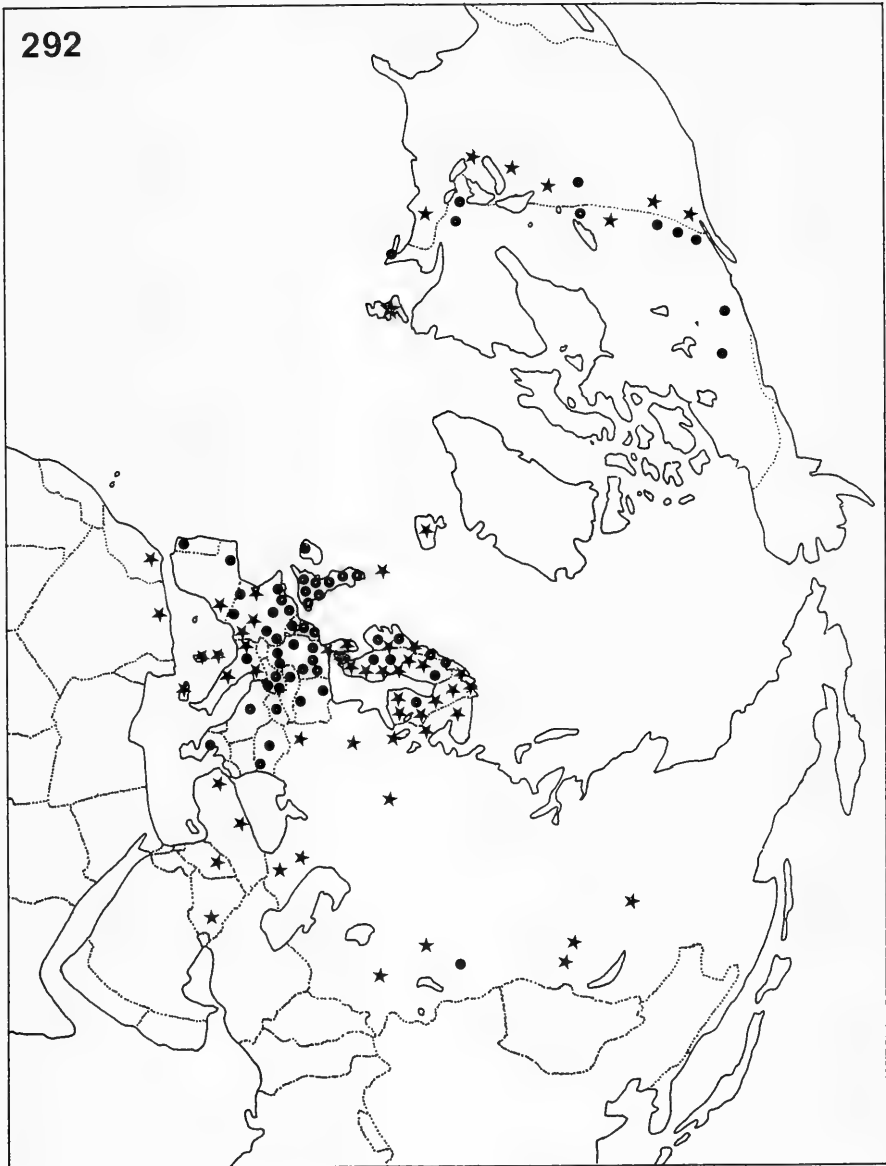
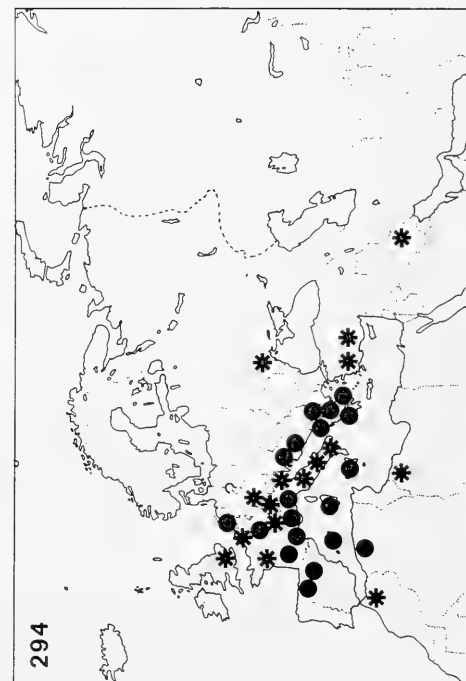
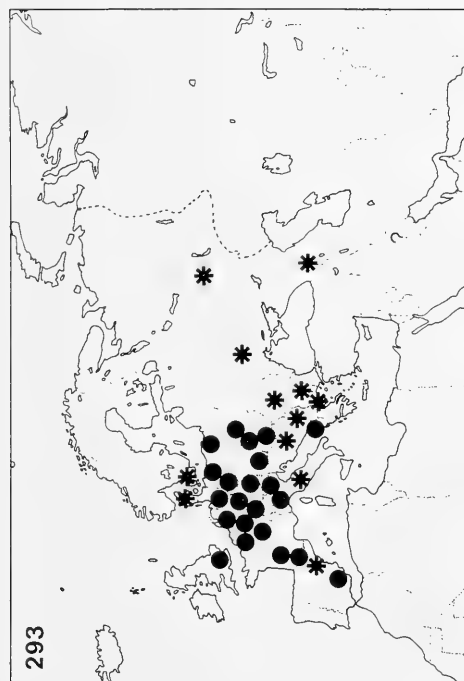
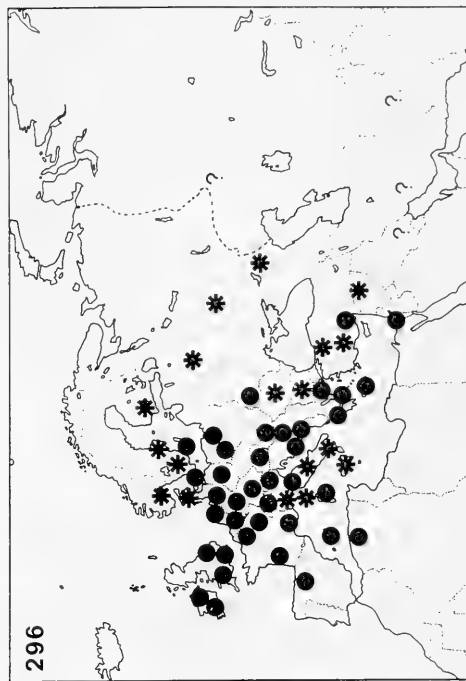
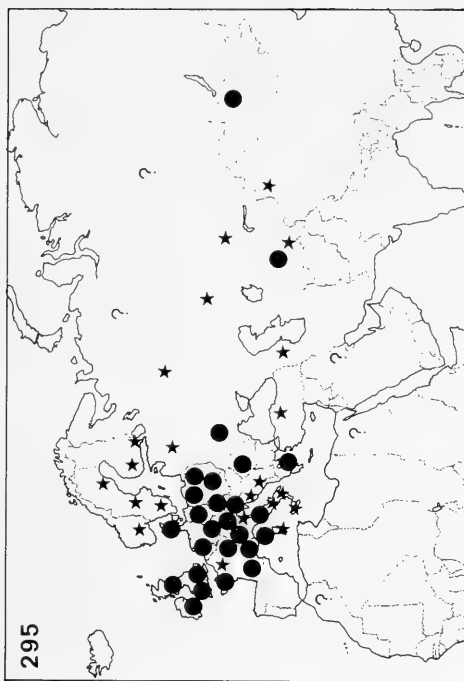
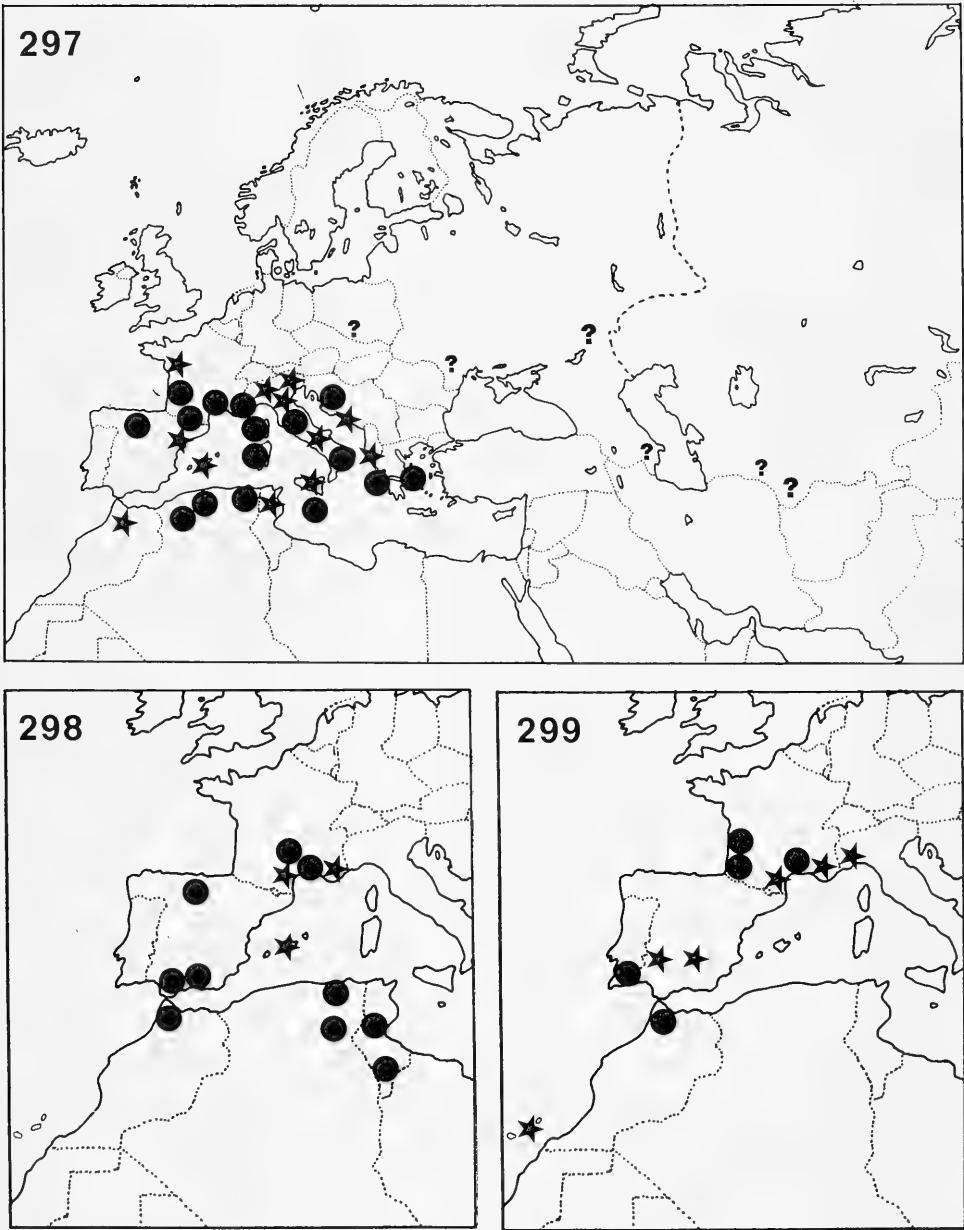


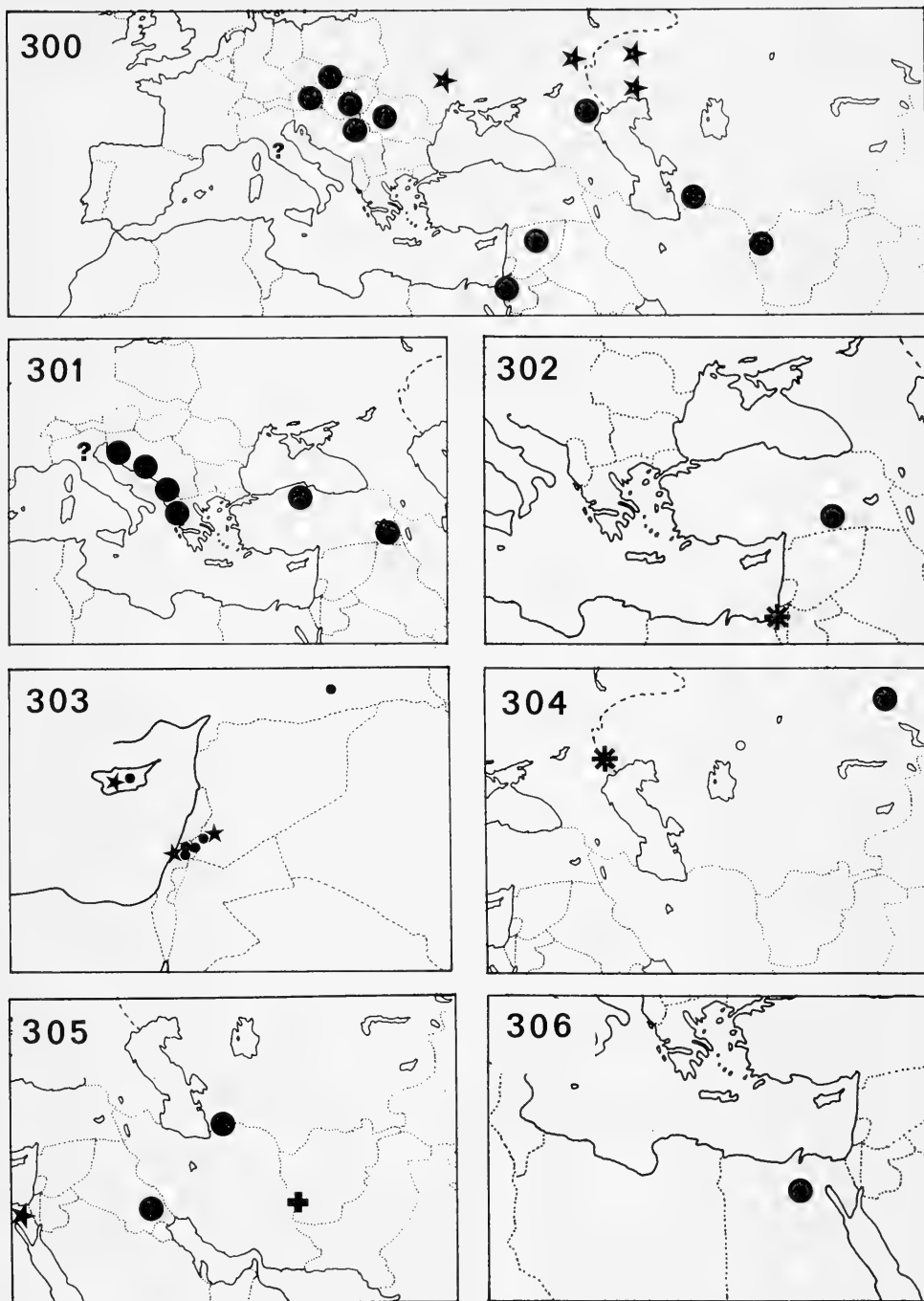
Fig. 292. Distribution of *Haliplus fulvus* (dots: material examined, stars: literature records).



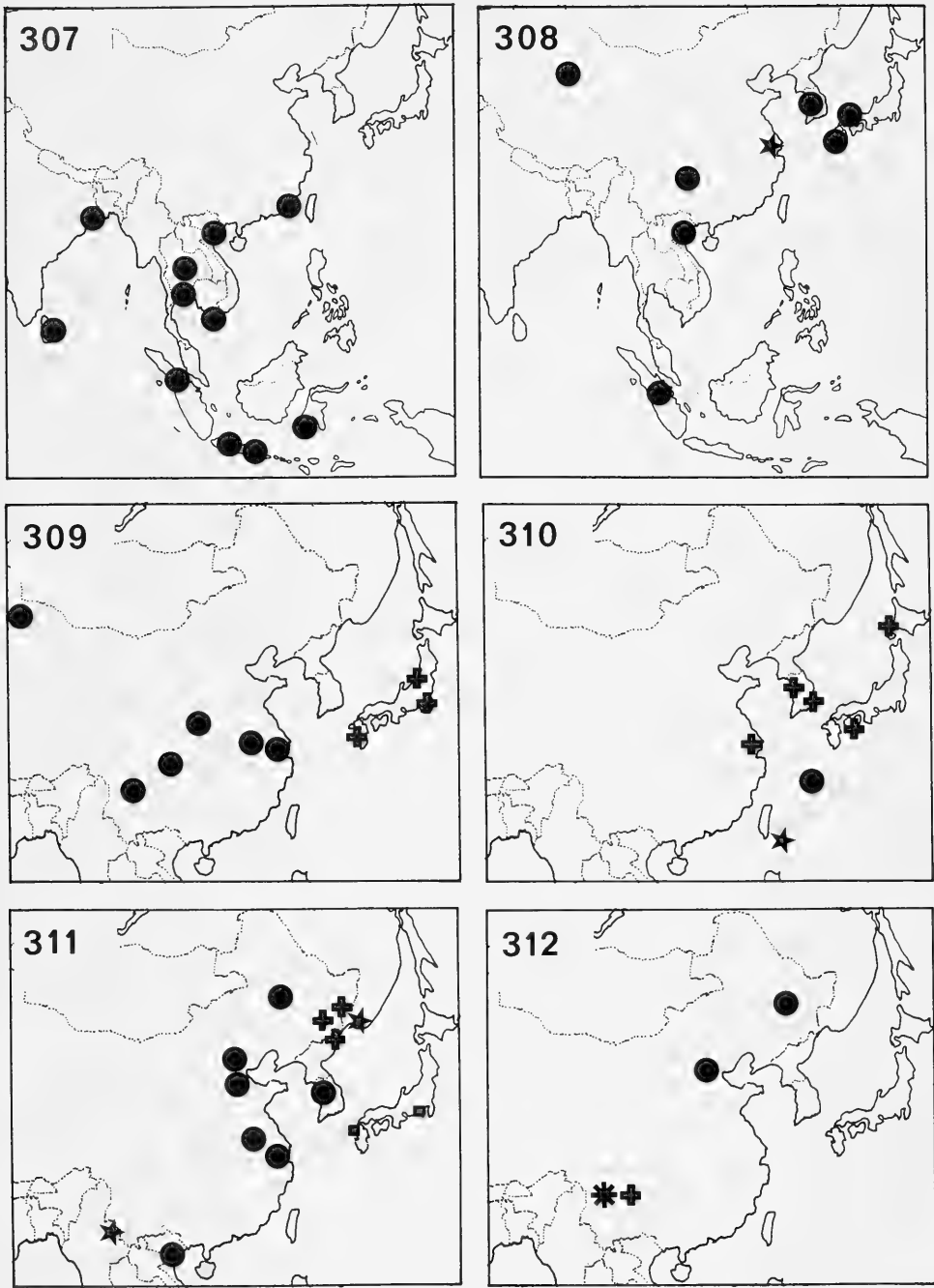
Figs. 293-296. Distribution of *Haliphys* spp. 293, *H. laminatus* (dots: material examined, stars: literature records); 294, *H. mucronatus* (dots: material examined, stars: literature records); 295, *H. flavicollis* (dots: material examined, stars: literature records); 296, *H. variegatus* (dots: material examined, stars: literature records).



Figs. 297-299. Distribution of *Haliplus* spp. 297, *H. guttatus* (dots: material examined, stars: literature records); 298, *H. andalusicus* (dots: material examined, stars: literature records); 299, *H. rubidus* (dots: material examined, stars: literature records).



Figs. 300-306. Distribution of *Haliphus* spp. 300, *H. maculatus* (dots: material examined, stars: literature records); 301, *H. dalmatinus* (dots: material examined); 302, *H. jaechi* (dot) and *H. kulleri* (star: material examined); 303, *H. gafnyi* (stars) and *H. ortalii* (dots); 304, *H. angusi* (dot) and *H. astrakanus* (star); 305, *H. abbreviatus* (dots: material examined, stars: literature records) and *H. villiersi* (cross: material examined); 306, *H. maculipennis* (dot: material examined).



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CEPHALACHORUTES GEN. N., A NEW GENUS OF TROPICAL NEANURIDAE (COLLEMBOLA)

Bedos, A. & L. Deharveng, 1991. *Cephalachorutes* gen. n., a new genus of tropical Neanuridae (Collembola). – Tijdschrift voor Entomologie 134: 145-153, figs. 1-22, tabs. 1-2. [ISSN 0040-7496]. Published 18 December 1991.

Cephalachorutes, a new genus of Neanuridae (Pseudachorutinae) Collembola, is described with five new species from Southeast Asia (*C. asiaticus* sp. n., *C. barthae* sp. n., *C. caecus* sp. n., *C. centurionis* sp. n., *C. pestilentiae* sp. n.) and one new species from Papua-Niugini (*C. murphyi* sp. n.). In addition, three species from Africa described in *Arlesia*, and one species from Nepal described in *Pseudachorutella* are moved to *Cephalachorutes*.

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Key words. – Collembola, Neanuridae, tropical forest.

Collections of forest soil fauna from Southeast Asia frequently contain small Pseudachorutinae (Neanuridae, Collembola) of unusual habitus, i. e. with short and wide body and head. Following the classical work of Massoud (1967), these species would have to be placed in either *Arlesia* or *Pseudachorutella*, according to the number of their eyes. More detailed morphological studies show, however, that, apart from their peculiar habitus, these forms share a set of unique characters which justify to isolate them in a new genus described below.

The terminology used is that of Deharveng (1983) for antennae and tibiotarsi; labium setae are named after Massoud (1967); dorsal setae are numbered after the row-system (Cassagnau 1974); however, the neanurian nomenclature of Deharveng (1983) is used when precise setal homologies are uncertain (th. II-III).

Abbreviations used in the descriptions: abd., abdominal segment; ant., antennal segment; d/m, ratio dens/mucro; S-setae, setae of type 'S'; th., thoracic segment.

The material is deposited in the collection of the Laboratoire de Zoologie, Université Paul Sabatier, Toulouse, France (LEIT) and in the Museum National d'Histoire Naturelle of Paris, France (MNHN).

Cephalachorutes gen. n.

Type species: *Cephalachorutes asiaticus* sp. n. (by present designation).

Description of the genus

Small size: 0.4 to 0.9 mm. Colour blue to white. Body short and wide (about half as wide as long), juvenile-like (fig. 1); 6th abdominal segment reduced.

Antennae (figs. 2-4). Antennae short and stocky; ant. III and ant. IV fused dorsally. Ant. IV with apical papilla reduced, either indistinct or simple (sometimes feebly trilobed), always fused to the apex of the article; organite 'or' globulous, in a ventro-apical position; seven well developed, thickened S-setae on ant. IV (S1 to S4, S7, S8 and MS); S7 much enlarged, overhanging the apex of ant. IV; S4 usually larger than other S-setae but smaller than S7; no s-microchaeta, MS as developed as other S-setae. The ant. III organ has moved to ventral side, with its guard-seta S5 shifted distally towards S8 of ant. IV; S3 close to S2. Ant. I with 7 setae.

Head (figs. 7, 9-12). Postantennal organ absent. 8+8 to 0+0 eyes. Buccal cone short and wide. Lines of setae A-B and C-D on labium arranged more or less perpendicularly. Labrum distally enlarged, like planaria-head. Labral chaetotaxy 4/3,4,2 with the 2 setae of the distal row and the lateral setae of the ante-distal row longer than others. Maxilla very thin, needle-like. Mandible thin, with 2 strong basal teeth and a distal comb of 4 to 12 small teeth (the 2 apical ones sometimes slightly larger).

Tergites (fig. 14). Ordinary setae very short. S-setae very long and thin, shorter on abd. IV. S-setae



Fig. 1. Habitus of *Cephalachorutes barthae* as an example of the genus. Length: 0.5 mm.

arranged after the standard hypogastrurian pattern (2+ms, 2/1,1,1,1,1 on each half-tergite from th. II to abd. V).

Sternites and body appendages (figs. 18, 19, 21). 1-2 + 1-2 setae on abd. II sternite. Tibiotarsal chaetotaxy: 8+11, 8+11, 7+11, or 7+11, 7+11, 6+11 when the seta M is absent. Ventral tube with

3+3 setae. Furcula well developed, tenaculum with 3+3 teeth, dens usually with 6 setae (only 3 setae in *C. microphthalmia*); mucro about half as long as dens, simple, similar to that of *Pseudachorutes parvulus*.

Derivatio nominis. – This genus is called after its unusually large and wide head (from the Greek noun *kephale* = head). Gender of the genus is masculine.

Discussion

The definition of *Cephalachorutes* relies primarily on the use of antennal chaetotaxy, which appears once again as an efficient taxonomic tool at suprageneric level in Neanuridae (Deharveng 1983).

Among Pseudachorutinae, *Cephalachorutes* gen. n. shares with *Arlesia* Handschin, 1942 and *Pseudachorutella* Stach, 1949 (sensu Massoud 1967) the following characters: postantennal organ absent, maxilla styliform, and mucrodens well developed.

Like the species of *Arlesia* sensu Massoud, the *Cephalachorutes* species have their seta MS of ant. IV of large size, whereas it is reduced to a microchaeta in most Pseudachorutinae and in the primitive family Hypogastruridae. In the type species of the genus *Pseudachorutella* (*Pasigillata*), this seta is also a microchaeta.

Cephalachorutes is easily differentiated from *Arlesia* and *Pseudachorutella* by the characters listed in tab.1. These last genera, formerly differentiated by the number of eyes (8+8 in *Pseudachorutella*, less in *Arlesia*, after Massoud 1967), cannot be separated any more on this ground as the species *Arlesia variabilis* Thibaud and Massoud, 1983 has 8+8 to 5+5 eyes. In fact, the complex *Arlesia-Pseudachorutella*, which includes a number of unrelated lines, has to be completely revised.

Table 1. Morphological differences between *Cephalachorutes* and *Arlesia/Pseudachorutella* complex.

	<i>Cephalachorutes</i>	<i>Arlesia/Pseudachorutella</i>
Size	less than 1 mm	usually more than 1 mm
Habitus	short and wide	long and relatively narrow
Ant. IV apical papilla	fused to the apex	not fused, trilobed
Position of ant. IV organite "or"	ventro-apical	dorso-apical
S7 (and often S4) of ant. IV vs other S-setae (figs. 3, 5)	thicker	not thicker
S2-S3 of ant. III organ	ventral	external
Ant. III: S2 length vs S2-S3 distance (figs. 4, 6)	$S2 > [S2-S3]$	$S2 < [S2-S3]^*$
Labrum shape	like planaria-head	different
Line of labial setae C-D (figs. 7 & 8)	more or less perpendicular to A-B	parallel to A-B
Mandible	2 big basal teeth and a distal comb of 4-12 small teeth	different

* observed in *Arlesia albipes* and in *Pseudachorutella asigillata*.

Some of the synapomorphies which define *Cephalachorutes* are unique among Pseudachorutinae. They are the habitus, at least in the most evolved species, the fusion of apical papilla to the apex of ant. IV, the position of the ant. IV organite 'or' (which has migrated beyond the apical papilla on the ventral side of the article), the hypertrophy of S7 and S4 on ant. IV and the labrum shape. The arrangement of the distal setae of labium is similar to that of *Kenyura* Salmon, 1954, indicating possible relationships between the two genera. The ventral position of ant. III organ is also observed in other genera, but in a different way. It is likely that other characters will prove to be discriminant, such as the maxilla arms structure (figs. 12, 13), but too few species are known in this respect.

Characters used in the descriptions of species

In addition to the characters, which are traditionally used for the taxonomy of Pseudachorutinae, the following chaetotaxic characters were found to vary between species:

- seta c3 on head
- number of dorso-external setae on th. II and th. III
- seta a2 on abd. IV
- seta a1 on abd. V: 2+2 (a1 present) or 1+1 setae (a1 absent) between – S-setae
- seta M on tibiotarsus

In the literature, the number of S-setae on ant. IV is stated to vary between species, but this is incorrect: there are always 7 S-setae on this article, but usually the thinnest have been overlooked and seta S5 of ant. III has been counted as an ant. IV S-seta.

Some of the chaetotaxic differences illustrated on figs. 15-17 might rather be individual variation than real interspecific differences: arrangement of setae is often variable on head and tergites (particularly on abd. VI), with frequent asymmetries.

Counting the number of eyes is an other serious difficulty for species identification in *Cephalachorutes*. Observation is easier if animals are treated by KOH before clearing.

Check-list of *Cephalachorutes*

- *C. minimus* (Massoud, 1963) **comb. n.** (from *Arlesia*); Angola.
- *C. delamarei* (Murphy, 1965) **comb. n.** (from *Arlesia*); Gambia.
- 7. *C. nakaoi* (Yosii, 1966) **comb. n.** (from *Pseudachorutella*); Nepal.
- *C. microphthalmus* (Barra, 1969) **comb. n.** (from *Arlesia*); Gabon.
- 6. *C. asiaticus* sp. n. (type species of the genus); Thailand, Indonesia, Philippines.

- 3. *C. barthae* sp. n.; Thailand.
- 2. *C. caecus* sp. n.; Thailand.
- 1. *C. centurionis* sp. n.; Thailand.
- 5. *C. murphyi* sp. n.; Papua-Niugini.
- 4. *C. pestilentiae* sp. n.; Thailand.

Arlesia pillaii Prabhoo, 1971 from India might belong to *Cephalachorutes*, but its description is insufficient.

Distribution, ecology

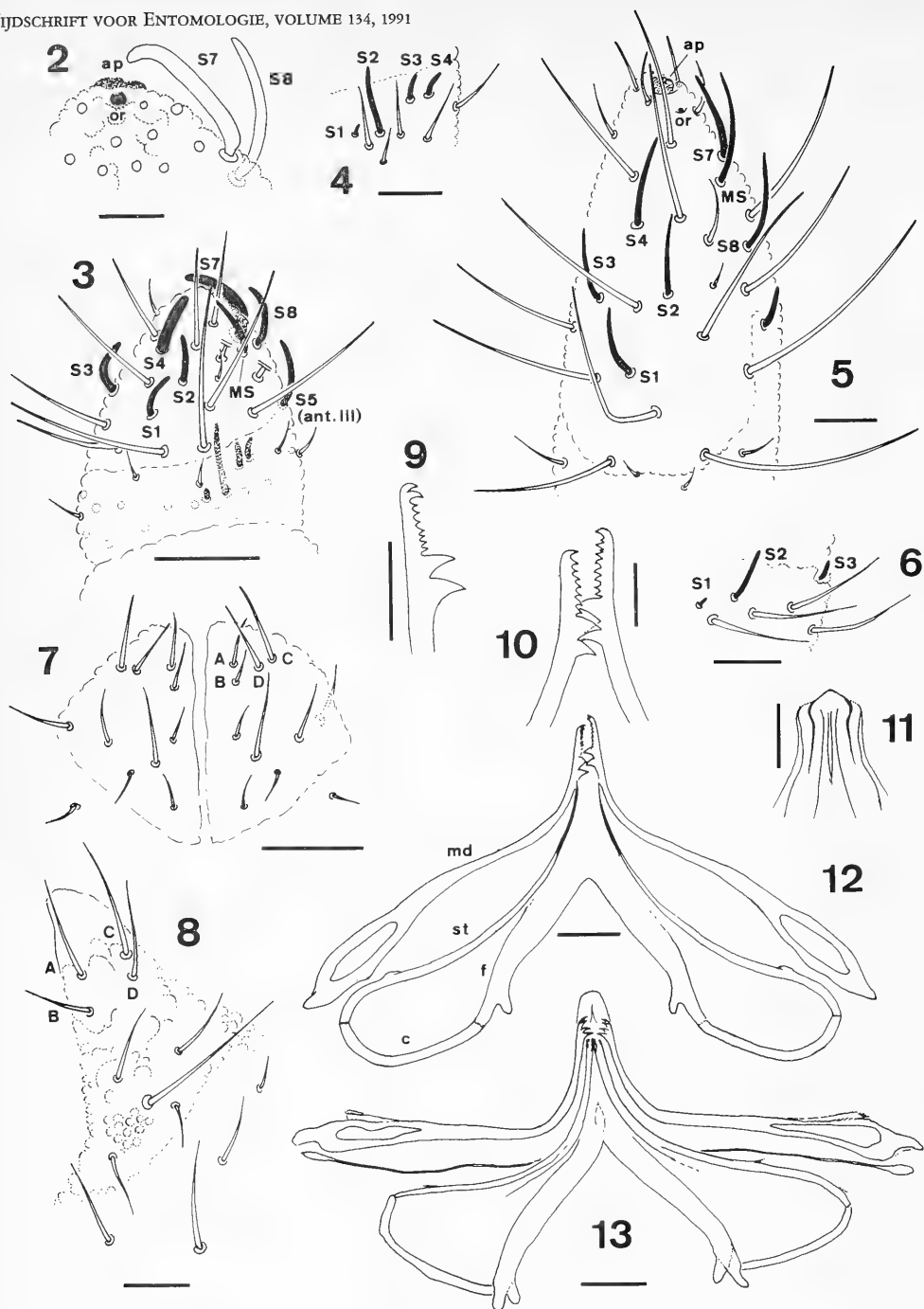
Cephalachorutes occurs in Africa, tropical Asia and Papua-Niugini, but not in tropical America. It is a rather frequent inhabitant of forest soils from sea level up to 3,500 m. Species with 4-8+4-8 eyes were collected from litter, whereas those with reduced eyes were mostly found in humus and soil.

Key to world species of *Cephalachorutes*

Additional characters for the species not redescribed in this paper are given in brackets.

- 1. Dens with 3 setae *C. microphthalmus*¹
[3-5+3-5 eyes, traces of pigment, claw un-
toothed, distal comb of mandible with 8-10
small teeth]
- Dens with 6 setae 2
- 2. 8+8 eyes 6. *C. asiaticus* sp. n.
- Less than 8+8 eyes 3
- 3. 5+5 eyes 4
- Less than 5+5 eyes 6
- 4. Distal comb of mandible with 4 small teeth
..... *C. minimus*
[pigment present, claw untoothed, description
unreliable for chaetotaxy]
- Distal comb of mandible with more teeth 5
- 5. Seta a2 present on abd. IV 7. *C. nakaoi*
- Seta a2 absent on abd. IV after original drawings
..... *C. delamarei*
[pale pigment, claw usually untoothed, some-
times claw I with tooth, distal comb of mandible
with 11-12 small teeth]
- 6. 4+4 eyes 7
- No eyes 9
- 7. 1+1 setae between S-setae on abd. V
..... 5. *C. murphyi* sp. n.

Note ¹: Here could be placed *Arlesia pillaii* Prabhoo, 1971: 4 setae on dens, 6+6 eyes, pigment present, claw with tooth, distal comb of mandible with 5-6 small teeth, S7 and S4 both thickened; however, the following characters given in the original description are not consistent with the definition of *Cephalachorutes*: 4+4 setae on ventral tube and only one big basal tooth on mandible.



Figs. 2-13. Differential characters on head between *Cephalachorutes* and *Arlesia*. - 2, Apex of ant. IV in *C. barthae* (ventral side, right antenna; ap: apical papilla; or: organite; circles: sockets of setae); 3, Ant. III-IV of *C. centurionis* (dorsal side, right antenna; S-setae and sockets of ordinary setae of ventral side in dots); 4, Ant. III organ in *C. barthae* (ventral side, right antenna); 5, Ant. III-IV of *A. albipes* (dorsal side, right antenna); 6, Ant. III organ in *A. albipes* (ventral side, right antenna); 7, Labium in *C. centurionis*; 8, Labium in *A. albipes*; 9, Mandible of *C. caecus*; 10, Mandibles of *C. barthae*; 11, Labrum in *C. barthae*; 12, Structure of mouthparts in *C. barthae* (c: cardo; f: fulcrum; st: stipa; md: mandible); 13, Structure of mouthparts in *A. albipes*. Scales: 10 μ (figs. 2, 9-11), 25 μ (figs. 3-8, 12), 50 μ (fig. 13).

- 2+2 setae between S-setae on abd. V 8
- 8. 3+S dorso-external setae on th. II and th. III 3. *C. barthae* sp. n.
- 2+S dorso-external setae on th. II and th. III 4. *C. pestilentiae* sp. n.
- 9. Tibiotarsus with seta M 1. *C. centurionis* sp. n.
- Tibiotarsus without seta M 2. *C. caecus* sp. n.

1. *Cephalachorutes centurionis* sp. n.

(figs. 3, 7, 14)

Type material. – Holotype, female, Thailand: Chiang Mai province, Doi Inthanon, 2550 m, soil in primary forest, 1.vi.1989, Deharveng and Bedos leg., sample CM 4 (LEIT). – Paratypes, Thailand: 1 male, 1 female, *ibid*, sample CM 6; 2 males, 2 females, 2 juv., *ibid*, humus in primary forest, 9.i.1981, Gouze leg., samples THA 93 and THA 94 (7 in LEIT, 2 in MNHN).

Description

Length 0.48–0.68 mm. Ratio length/width = 2.3. Colour whitish sometimes with slight traces of grey pigment.

Antennae. Ant. IV with apical papilla entire, fused to the apex; S-setae large and thick; S7 banana-like and larger than others, overhanging the apex of the segment; S4 smaller than S7 but larger than other S-setae. Setae S2 and S5 of ant. III subequal to S8 of ant. IV; on ant. III, S2 is 5 times as long as S3.

Head. No ocelli visible, but sometimes 1+1 minute black ocular spots. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 9–10 small teeth.

Tergites. On th. II and th. III, 3+S dorso-external setae. On abd. IV, a2 absent. On abd. V, 2+2 ordinary setae between S-setae.

Body appendages. Seta M present on tibiotarsus. Claw without tooth. Dens with 6 setae. Mucro less than half as long as dens ($d/m = 2.1\text{--}2.3$).

Derivatio nominis. – This species is named after our friend Alain Gouze, firemen officer, who collected the first specimens of this species (from the Latin noun in genitive case *centurio* = commandant).

Discussion. – Cf *C. caecus*.

2. *Cephalachorutes caecus* sp. n.

(fig. 9)

Type material. – Holotype, male juvenile, Thailand: Chiang Mai province, Doi Chiang Dao, 950 m, humus in forest, 4.vii.1985, Deharveng leg., sample DC 67 (LEIT). – Paratypes, Thailand: 1 juv., *ibid*, 1000 m, soil in forest,

4.vii.1985, Deharveng leg., sample DC 56; 1 female juv., 3 juv., *ibid*, 500 m, wet litter in forest, 17.xii.1980, Deharveng leg., sample THA 4 (other specimens in alcohol); 1 female, Chiang Mai province, Doi Mae Tho, 1300 m, humus in forest, 14.vii.1985, Deharveng and Bedos leg., sample CL 11 (4 in LEIT, 2 in MNHN).

Description

Length 0.55–0.65 mm. Ratio length/width = 2.2. Pigment absent.

Antennae. Ant. IV with apical papilla slightly knobbed, fused to the apex; S7 large, fairly thicker than S4; other S-setae thinner and rather long. Setae S2 and S5 of ant. III are subequal to S8 of ant. IV; on ant. III, S2 is 4.5 times as long as S3.

Head. No eyes, no ocular spots of pigment. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 8–9 small teeth, the 2 apical ones relatively stronger.

Tergites. On th. II and th. III, 3+S dorso-external setae. On abd. IV, a2 absent. On abd. V, 2+2 ordinary setae between S-setae.

Body appendages. Seta M absent on tibiotarsus. Claw without tooth. Dens with 6 setae. Mucro more than half as long as dens ($d/m = 1.8\text{--}1.9$).

Derivatio nominis. – This species is named for the absence of eyes (from the Latin adjective *caecus* = blind).

Discussion. – *C. centurionis* and *C. caecus* are the only species of the genus devoid of eyes. They have also the most developed S-setae on ant. IV and ant. III. They differ by the size of 2 apical teeth of the distal comb of the mandible (stronger in *C. caecus*), the tibiotarsal seta M (present in *C. centurionis*, absent in *C. caecus*) and the ratio dens/mucro (higher in *C. centurionis*).

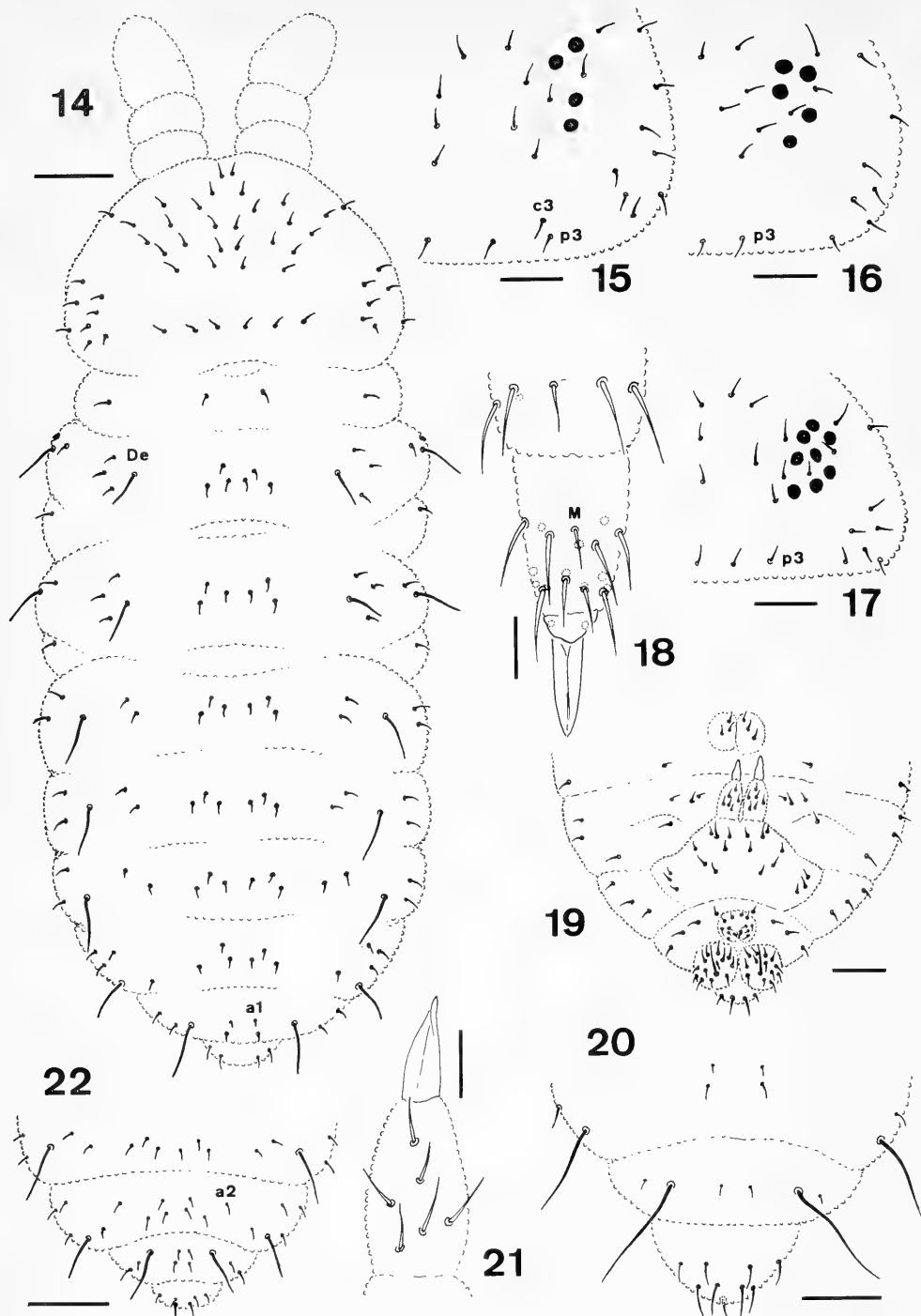
3. *Cephalachorutes barthae* sp. n.

(figs. 1, 2, 4, 10, 11, 12, 19)

Type material. – Holotype, male, Thailand: Chiang Mai province, Doi Mae Tho, 1300 m, in litter forest, 14.vii.1985, Deharveng and Bedos leg., sample CL 17 (LEIT). – Paratypes, Thailand: 1 female, same sample; 1 male, 2 juv., *ibid*, sample CL 18; 1 female, Chiang Mai province, Doi Inthanon, 2500 m, humus in primary forest, 2.i.1981, Deharveng leg., sample THA 72; 1 juv., *ibid*, 2000 m, humus in primary forest, 2.i.1981, Deharveng leg., sample THA 77; 2 juv., *ibid*, 1700 m, litter in primary forest, 1.vi.1989, Deharveng and Bedos leg., sample CM 34 (5 in LEIT, 2 in MNHN).

Description

Length 0.55–0.70 mm. Ratio length/width = 2. Colour blue.



Figs. 14-22. Differential characters between species of *Cephalachorutes*. - 14, Dorsal chaetotaxy of *C. centurionis*; 15, Ocular area of *C. pestilentiae*; 16, Ocular area of *C. nakaoti*; 17, Ocular area of *C. asiaticus*; 18, Chaetotaxy of leg II in *C. asiaticus* (ventral side; dotted circles: sockets of dorsal setae); 19, Ventral chaetotaxy of *C. barthae*; 20, Abd. IV-VI of *C. murphyi*; 21, Mucrodens of *C. asiaticus*; 22, Abd. III-VI of *C. asiaticus*. Scales: 10 μ (figs. 18, 21), 25 μ (figs. 15-17), 50 μ (figs. 14, 19, 20, 22).

Table 2. Differential characters between *C. barthae*, *C. pestilentiae* and *C. murphyi*.

	<i>barthae</i>	<i>pestilentiae</i>	<i>murphyi</i>
Body length/width	2	2	2.3
Seta c3 on head	absent	present	absent
Dorso-external setae on th. II-III	3+S	2+S	2+S
Seta a2 on abd. IV	absent	present	absent
Seta a1 on abd. V	present	present	absent

Antennae. Ant. IV with apical papilla entire but knobbed, fused to the apex; S-setae rather thin, S4 and particularly S7 thicker. Seta S5 of ant. III shorter than S8 of ant. IV; on ant. III, S2 subequal to S5 and 3 times as long as S3.

Head. 4+4 eyes, sometimes not obvious. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 8-10 small teeth.

Tergites. On th. II and th. III, 3+S dorso-external setae. On abd. IV, a2 absent. On abd. V, 2+2 ordinary setae between S-setae.

Body appendages. Seta M absent on tibiotarsus. Claw with a minute inner tooth, sometimes indistinct. Dens with 6 setae. Mucro more than half as long as dens ($d/m = 1.7-1.9$).

Derivatio nominis. – This species is named to thank Florence Barth for her drawing of the *Cephalachorutes* habitus (fig. 1).

Discussion. – Cf *C. murphyi*.

4. *Cephalachorutes pestilentiae* sp. n. (fig. 15)

Type material. – Holotype, female, Thailand: Chiang Mai province, north of Ban Muang Ngai, 600 m, litter in forest, 4.vi.1989, Deharveng and Bedos leg., sample CM 59 (LEIT). – Paratypes, Thailand: 7 females, 2 juv., same sample (numerous specimens in alcohol) (7 in LEIT, 2 in MNHN).

Description

Length 0.70-0.85 mm. Ratio length/width = 2. Colour blue.

Antennae. Ant. IV with apical papilla knobbed, fused to the apex; S4 and particularly S7 thicker than other S-setae. Setae S2 and S5 of ant. III subequal to S8 of ant. IV; on ant. III, S2 is more than 3 times as long as S3.

Head. 4+4 eyes (2+2 ocular spots well distinct in alcohol). Seta c3 present; more setae on lateral area than in other species. Mouthparts typical of the genus; distal comb of mandible with 8-9 small teeth.

Tergites. On th. II and th. III, only 2+S dorso-external setae. On abd. IV, a2 present. On abd. V,

2+2 ordinary setae between S-setae.

Body appendages. Seta M absent on tibiotarsus. Claw with a minute inner tooth. Dens with 6 setae. Mucro more than half as long as dens ($d/m = 1.7-1.8$).

Derivatio nominis. – The name of the species refers to its type locality, a doline with a very high level of carbon dioxide up to 5% (from the Latin noun in genitive case *pestilentia* = bad air).

Discussion. – Cf *C. murphyi*.

5. *Cephalachorutes murphyi* sp. n. (fig. 20)

Type material. – Holotype, female, Papua-Nuigini: Wau, Bulldog road, 2600 m, in litter of moss forest, 1.xii.1979, Deharveng leg., sample PNG 266 (LEIT). – Paratypes, Papua-Nuigini: 1 male, 1 female, Wau, Bulldog road, 2650 m, Rhododendron litter, 1.xii.1979, Deharveng leg., sample PNG 263 (LEIT).

Description

Length 0.75-0.90 mm. Ratio length/width = 2.3. Colour blue. Habitus less thick-set than the other species of the genus. Abd. VI not hidden under abd. V.

Antennae. Ant. IV with apical papilla knobbed, fused to the apex; S4 and particularly S7 thicker than other S-setae, which are long and thin. Seta S5 of ant. III half as long as S8 of ant. IV; on ant. III, S2 slightly longer than S5 and less than 3 times as long as S3.

Head. 4+4 eyes not well distinct. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 9-10 small teeth.

Tergites. Dorsal chaetotaxy very reduced, difficult to observe on our material. On th. II and th. III, only 2+S dorso-external setae. On abd. IV, a2 absent and only 1+1 setae in the p-row between S-setae. On abd. V, 1+1 ordinary setae between S-setae.

Body appendages. Seta M absent on tibiotarsus. Claw with one obvious inner tooth. Dens with 6 setae. Mucro half as long or slightly longer than dens ($d/m = 1.8-2$).

Derivatio nominis. – This species is named in honour of Prof. Murphy who noticed in 1965 that species from Africa should be separated from the neotropical group of *Arlesia*.

Discussion. – Three species of *Cephalachorutes* have 4+4 eyes: *C. barthae*, *C. pestilentiae* and *C. murphyi*. They are also devoid of seta M on tibiotarsus. They can be differentiated after table 2. In addition, *C. microphthalmus* has 3 to 5 eyes on each side, but the species is distinguished easily from the latter by its dens with 3 setae instead of 6.

6. *Cephalachorutes asiaticus* sp. n. (figs. 17, 18, 21, 22)

Type material. – Holotype, male, Thailand: Chiang Mai province, Ban On Luoi, 500 m, bamboo litter, 20.vii.1985, Deharveng leg., sample CL 44 (LEIT). – Paratypes, Thailand: 2 males, 1 female, 5 juv., same sample (other specimens in alcohol) (6 in LEIT, 2 in MNHN).

Other material. – The following material has been considered as *C. asiaticus*: Indonesia: 1 male, Sulawesi Selatan, Maros district, Kappang, Gua Salukkan Kallang (cave), 200 m, flood debris, 14.vii.1986, sample INDO 142; 2 juv., Sulawesi Selatan, Maros district, Kappang, 300 m, in litter of Lantana bushes, 8.vii.1989, Deharveng and Bedos leg., sample SULS 35 (LEIT). – Philippines: 2 males, 3 females, 2 juv., Mindoro Island, Puerto Galera, 150 m, litter in forest, 29.xii.1979, Deharveng leg., sample PHI 116 (LEIT).

Description

Length 0.55–0.65 mm. Ratio length/width = 2.3. Colour blue.

Antennae. Ant. IV with apical papilla fused to the apex; S7 thicker than other S-setae; S2 slightly larger than S3; other S-setae fairly smaller. Seta S5 of ant. III shorter than S8 of ant. IV; on ant. III, S2 subequal to S5 and less than 3 times as long as S3.

Head. 8+8 eyes. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 9–10 small teeth.

Tergites. On th. II and th. III, 3+S dorso-external setae. On abd. IV, a2 present. On abd. V, 2+2 ordinary setae between S-setae.

Body appendages. Seta M present on tibiotarsus. Claw with a minute inner tooth. Dens with 6 setae. Mucro half as long as dens ($d/m = 2$).

Derivatio nominis. – This species is named for its large repartition through the tropics in South east Asia.

Discussion. – *C. asiaticus* is the only species of *Cephalachorutes* with 8+8 eyes. As other primitive character, this species has, with *C. nakaoi*, the most complete chaetotaxy of tergites in the genus. An-

tennal S-setae are relatively poorly developed. Specimens from Indonesia and Philippines have been referred to *C. asiaticus*, but slight differences in relative width of the body and relative length of mucro were observed with the Thai material.

7. *Cephalachorutes nakaoi* (Yosii, 1966) comb. n. (fig. 16)

Material (type material not examined). – Nepal: 1 male, 1 female, 6 juv., Marsyandi valley, between Chame and Tarapani, 2450 m, in litter and humus of *Quercus glauca* and *Rhododendron*, 4.x.77, Deharveng leg., sample Nep 77B-118 (LEIT).

Description

Length 0.60–0.70 mm. Ratio length/width = 2.2. Colour blue.

Antennae. Apical papilla of ant. IV with 3 lobes more or less distinct, fused to the apex; S4 and particularly S7 thicker than other S-setae, which are relatively slender. Seta S5 of ant. III shorter than S8 of ant. IV; on ant. III, S2 slightly longer than S5 and 3 times as long as S3.

Head. 5+5 ocelli, sometimes not well distinct. Seta c3 absent. Mouthparts typical of the genus; distal comb of mandible with 7–12 small teeth.

Tergites. On th. II and th. III, 3+S dorso-external setae. On abd. IV, a2 present. On abd. V, 2+2 ordinary setae between S-setae.

Body appendages. Seta M present on tibiotarsus. Claw with one inner tooth, minute or sometimes indistinct. Dens with 6 setae. Mucro half as long as dens or slightly smaller ($d/m = 2-2.2$).

Discussion. – The original description of the species by Yosii (1966) differs in the apical papilla of ant. IV being conspicuous and distinctly trilobed, whereas it is variable but fused to apex in our material. Other characters are concordant, but chaetotaxic information is lacking for the type specimens which had lost the S-setae on body and antennae, according to the author. *C. nakaoi* has 5+5 eyes like the African species (*C. minimus*, *C. delamarei* and *C. microphthalmus*). Available differential characters are few, because the chaetotaxy of these last species is poorly known. The main differences are given in the key.

ACKNOWLEDGEMENTS

We should like to thank J. M. Thibaud for the loan of *Arlesia* slides from the Petites Antilles.

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BOOK ANNOUNCEMENTS AND REVIEWS

Kime, R. D., 1990. A provisional atlas of European Myriapods. Part 1. – Fauna Europaea Invertebrata, European Invertebrate Survey, Volume 1: 1-109. Luxembourg. [ISSN 0257-7038, obtainable from Musée national d'Histoire naturelle, Luxembourg. Price Lux. Franc 600].

This is the first volume of Fauna Europaea Invertebrata, a newly started serial work issued by the European Invertebrate Survey. The E.I.S. promotes the publication of distribution maps on an international scale. The present atlas is a good example. It is also the first volume of a series of atlases on the Myriapoda of which nearly 2000 species occur in Europe. This first volume comprises maps for 50 species, all Diplopods, for which the collection of data had been completed and all data checked. The maps are based on published and unpublished records, all from reliable sources, such as collections in natural history museums, publications by authors of repute and recent specialists' fieldwork. Doubtful records have not been included. Other maps will be published in due course in batches of 50 or more.

The European base map with 50 × 50 km squares is used for the purpose, giving appropriate detail for such a large area. Even on this scale not all records could be correctly situated because the locality data, from the literature or on the labels, were too imprecise, a clear hint to collectors and authors to be more accurate.

The atlas is an example of international cooperation. No less than 40 cooperators from 18 countries are acknowledged for their help with providing records or collections. Despite this seemingly fair coverage of Europe the author recognizes obvious gaps in the distributions which are most likely the result of geographically uneven collecting activities in the past. The maps for this good reason have a provisional character. The usual visualization of older against newer records was not carried through in this project as the records are equally unevenly spread in time. There never were many Myriapod specialists and their collecting activities in a certain area often have a snapshot character with nothing known before or after. The author expresses his hope that the present maps will stimulate collecting in those areas which so far were neglected or undersampled, or were inventoried long ago.

The format of the atlas is squarish, an adaptation to the format of the maps. For each species the opposite page gives relevant ecological information on habitat and distribution range. Apart from the authorship of the species there are no literature references. A complete bibliography will be pub-

lished later as a separate volume. We may call this first volume a must for all Myriapodologists and also for anybody interested in the zoogeography of Europe.

[P. J. van Helsdingen]

Cherepanov, A. I., 1990. Cerambycidae of Northern Asia. – E. J. Brill, Leiden &c. Volume 1: Prioninae, Disteniinae, Lepturinae, Aseminae. 642 pp, 296 figs. [ISBN 90 04 09140 8] Hfl. 225.-; volume 2 (in two parts): Cerambycinae. 292 and 354 pp, 133 and 153 figs. [ISBN 90 04 09404 0] Hfl. 270.-; volume 3 (in two parts): Lamiinae. 300 and 308 pp, 120 and 133 figs. [ISBN 90 04 09140 8] Hfl. 290.-. All cloth with dust jacket.

A description of the morphology, geographic distribution, and biology of cerambycid beetles (Coleoptera: Cerambycidae). Keys to taxa based on different developmental stages are presented here for the first time, host relationships examined, and the life cycle and ecology of each species assessed. Volume 1 includes four subfamilies, comprising 124 species, volume 2 includes 108 species, and volume 3 152 species. The data for these books were obtained during field and laboratory investigations over wide expanses of Siberia, the Urals and the Far East.

The adults of all species, and larvae and pupae of many species are illustrated. The books are translations of the original Russian 'Usachi Severnoi Azii' published from 1979 onwards. It is most fortunate that the knowledge about these beetles has become available in English. Descriptions and biological notes are detailed and certainly useful for e.g. workers in plant protection. Unfortunately, the quality of reproduction (especially of the illustrations) is inadequate.

[J. van Tol]

Veeresh, G. K., B. Mallik & C. A. Viraktamath (eds.), 1990. Social insects and the environment. Proceedings of the 11th International Congress of IUSI 1990. – E. J. Brill, Leiden &c. 765 pp. [ISBN 90 04 09316 8]. Cloth in dust jacket. Hfl. 150.-.

This volume includes 370 papers presented by leading scientists at the 11th Congress of the International Union for the Study of Social Insects at Bangalore, from August 5-11, 1990. The papers are classified into 30 sections related to the symposia papers of the Congress. These cover various frontiers of research on social insects such as evolution of sociality, polygyny, social polymorphism, kin-recognition, kin-selection, foraging strategies, reproductive strategies, biogeography and phylogenetics of bees and ants pollination ecology and management of pestiferous social insects.

The texts are unrefereed, unedited abstracts of the papers presented and printed as camera-ready copy. [Mainly from information by the publisher]

A REVIEW OF THE PHILIPPINE SPECIES OF THE *COROEBUS* GORY & LAPORTE GENUS-GROUP (COLEOPTERA, BUPRESTIDAE)

Bellamy, C. L., 1991. A review of the Philippine species of the *Coroebus* Gory & Laporte genus-group (Coleoptera, Buprestidae). – Tijdschrift voor Entomologie 134: 155-176, figs. 1-67. [ISSN 0040-7496]. Published 18 December 1991.

The Philippine genera and species of the *Coroebus* generic group are reviewed. Five species of *Coroebus* are identified: *coelestis* Saunders, *spinosus* (Fabricius), *hastanus* Gory & Laporte, *albiventris* sp. n. and *bivestitus* sp. n. Five species of *Cisseicoraebus* are recognized: *grandis* (Kerremans), *pullatus* (Saunders) comb. n., *piperi* (Fisher) comb. n., *cisseoides* (Saunders) comb. n. and *bicoloratus* sp. n. *Philocoroebus* gen. nov., is described for *azureipennis* (Obenberger) comb. n., *banabaoensis* (Obenberger) comb. n., *meliboeiformis* (Saunders) comb. n., *cyaneoviridis* Fisher comb. n., and seven new species: *maquilingensis* sp. n., *purpureus* sp. n., *samarensis* sp. n., *elongatus* sp. n., *alius* sp. n., *adamantinus* sp. n. and *pseudocisseis* sp. n. The first Philippine species of *Cisseis*: *aquilonia* sp. n. and *Hypocisseis*: *philippinensis* sp. n., are described. The second Philippine species of *Vanroonia*: *luzonica* sp. n. is described. Keys are presented to separate the Philippine genera of the *Coroebus* group and the species of *Coroebus*, *Cisseicoraebus* and *Philocoroebus*.

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Key words. – Philippines, Buprestidae, *Coroebus*, taxonomy.

The eventual understanding of the genera and relationships within the large, virtually cosmopolitan tribe Coroebini is dependent upon the correct definition and species placement within or outside the type-genus *Coroebus* Gory & Laporte. The coroebine element of the Philippine Islands is particularly exciting due to its position biogeographically as the transition zone between the disparate faunas of southeast Asian, Malesian and Australasian regions.

Some of the taxa described herein were separated and apparently recognized as new by W. S. Fisher (Department of Entomology, USNM), but he never found the opportunity to realize his apparent intentions following the three main contributions to the Philippine buprestid fauna (Fisher 1921, 1922, 1926).

Label data are presented verbatim with commas inserted to separate data from individual lines and the "/" used to separate data from individual labels. Parenthetical information is added for clarity.

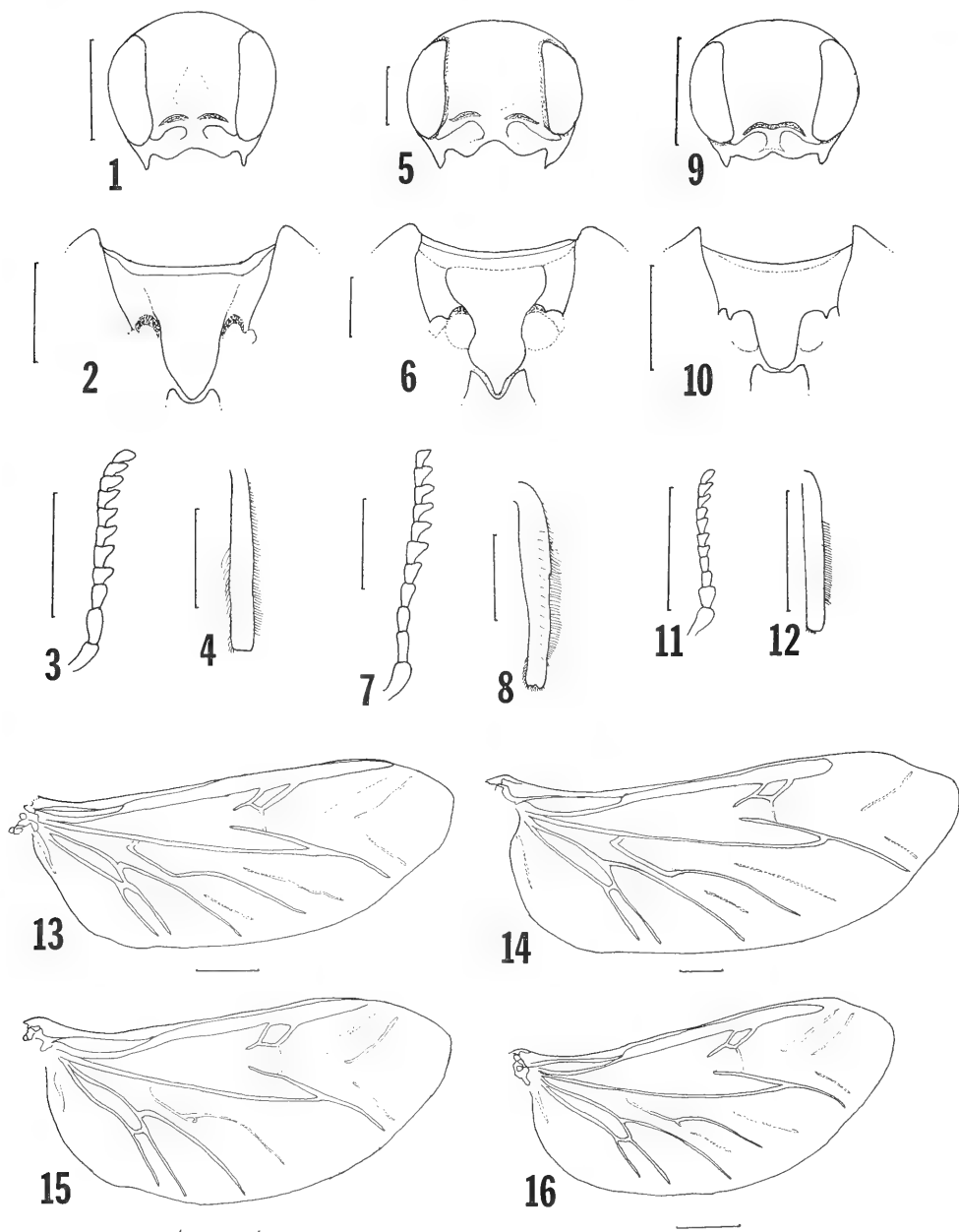
The following acronyms are used to indicate the various collections which house and/or loaned material for this study: BMNH, The Natural History

Museum, London, England; BPBM, B. P. Bishop Museum, Honolulu, Hawaii, U.S.A.; NMPC, National Museum, Prague, Czechoslovakia; NSMT, National Science Museum, Tokyo; USNM, National Museum of Natural History, Washington, D.C. and VCLP, Visayas State College of Agriculture, Leyte, Philippines.

A few morphometric abbreviations are used in the text as follows: L/W = total length versus width ratio, taken from greatest anterior extension of head to elytral apex; PN W/L = pronotal width versus length ratio; and PS L/W = prosternal length versus width ratio, both using maximum widths and lengths.

I was unable to make contact with or secure the loan of material from most of the Philippine collections and imagine that there is probably additional material awaiting study and description in the future.

It will eventually make sense and be necessary to comment on the phylogenetic relationships of the Philippine Coroebini. However, as there remain numerous undescribed coroebine taxa in the USNM



Figs. 1-16. Key figures for Philippine *Coroebus* generic group, head (frontal aspect), thoracic sternites (ventral aspect), antennae, metatibiae and hind wings. – 1-4, 13, *Coroebus hastanus*; 5-8, 14, *Cisseicoroebus grandis*; 9-12, 15, *Philocoroebus azureipennis*; 16, *P. alius* sp. n. (scale lines = 1 mm).

collections and probably others, e. g. several new species of *Brachycoroebus* Kerremans from Basilan and Mindanao and new species of both *Cryptodactylus* Deyrolle and *Neotoxoscelus* Fisher, it is certainly beyond both the scope and intent of this paper. This work has the sole purpose of defining and describing the taxa belonging to the *Coroebus* genus-group and as a starting point, I have emended the generic key recently presented in the first part of this series (Bellamy 1990).

KEY TO THE PHILIPPINE GENERA OF THE COROEBUS GROUP

1. Body generally elongate; pronotum without prelaral carinae; prosternum generally flattened, broadly excavated dorsad of procoxae 2
- Body more or less ovoid or elongate ovoid; pronotum with (e.g. figs. 38, 39) or without prelaral carinae; prosternum generally more longitudinally convex and not so excavated 6
2. Mentonniere absent, anterior margin of prosternum entire or feebly concave 3
- Mentonniere present, anterior margin of prosternum with either a single broad lobe or bilobed 4
3. Prosternum with disc produced ventrally, more or less forming a 'V' shape, with anterior margin concave between two projected lateral angles; pygidium without median spine and not visible past elytral apices
..... *Coraeobosoma* Obenberger
- Prosternum more or less entire, anterior margin evenly transverse; pygidium with single projecting medial tooth or spine visible between and past elytral apices (e.g. fig. 25)
..... *Coroebus* Gory & Laporte
4. Head and pronotum uneven, tuberculate *Vanroonia* Obenberger
- Head and pronotum even, entire 5
5. Elytra unicolorous; parts of pronotum, elytra and ventral surface clothed with dense spots, patches or fasciae of white or yellowish pubescence *Cisseicoroebus* Kerremans
- Elytra with patterns of blue spots and fasciae; pubescence, when present, not in dense concentrations, much less conspicuous
..... *Obenbergerula* Hoscheck
6. Lateral marginal carinae of pronotum entire, not crenulate or otherwise interrupted 7
- Lateral marginal carinae of pronotum crenulate
..... *Philocoroebus* gen. n.
7. Pronotal lateral carinae, when viewed from above, not visible past premarginal carinae; pronotum more or less flattened
..... *Cisseis* Gory & Laporte

- Lateral carinae of pronotum fully visible from above; pronotal disc uneven or convex medially 8
- 8. Pronotum more or less evenly convex medially; dorsal coloration apparently mimetic, nitid green with elytral bluish purple spots; elytra without any squamiform setal concentrations *Anocisseis* Bellamy
- Pronotum uneven, with elevated tubercles or costae; dorsal coloration apparently cryptic, somber with irregular iridescent reflections; elytra with irregular concentrations of squamiform setae *Hypocisseis* Thomson

TAXONOMIC PART

Genus *Coroebus* Gory & Laporte

Coroebus Gory & Laporte, 1839: 1. – Baer 1886: 126; Saunders 1871: 104; Kerremans 1903: 231; Schultze 1916: 56; Fisher 1921: 405; Obenberger 1935: 817; Bellamy 1985: 425; 1990: 691. – Type-species: *Buprestis undatus* Fabricius [as designated: Descarpentries & Villiers 1967].

Remarks. – The Philippine species of *Coroebus* have been considered differently in the past. I have decided to narrow the definition in concert and comparison with the type-species and several close relatives from the Palaearctic fauna. This then serves as the starting point and foundation for the subsequent descriptions and new combinations below.

Key to the Philippine species of *Coroebus*

1. Dorsal surface unicolorous, appearing glabrous, setae very short and sparse, not concentrated into patches or fasciae (Mindanao)
..... *C. coelestis* Saunders
- Dorsal surface with setae concentrated into transverse fasciae or patches 2
2. Dorsal surface multicolorous, at least when viewed from different angles, some colours, and at some angles, very bright 3
- Dorsal surface unicolorous, ground colour quite somber 5
3. Pronotum, more or less, unicolorous, green or deep blue; elytral disc bright green or bluish green, marginal areas black with strong deep blue or violet reflections; elytral with two transverse setose fasciae, one near apical 1/3 and the other just before apical margin (Leyte, Mindanao) *C. spinosus* (F.)
- Pronotum, more or less, bicolorous, disc deep green and basolateral portion reddish cupreous, cupreous or bright green; elytral disc nitid black, marginal areas in basal 1/2 and entire apical 1/4 green; elytra with a two pairs of setal

- patches on disc of middle 1/3 before single setose fascia at apical 1/3 (Luzon, Mindanao, Negros, Polillo, Samar) *C. hastanus* Deyrolle
4. Pronotum subglabrous, disc flattened; dorsal colour blue; elytra with two pairs of white setose patches and two obliquely transverse fasciae (Negros) *C. albivestitus* sp. n.
- Pronotum with long, recumbent setae, disc convex; dorsal colour subnitid black; elytra with white setose patches and one wide fascia past apical 1/3 and a longitudinal band of testaceous setae extending along suture (Negros) *C. bivestitus* sp. n.

***Coroebus hastanus* Gory & Laporte**
(figs. 1-4, 13, 18-19)

Coroebus hastanus Gory & Laporte, 1839: 10. – Baer 1886: 126; Kerremans 1903: 233; Schultze 1916: 56; Obenberger 1935: 830.

Material. – 24 examples (USNM): Luzon, Tayabas Pr., Mt. Dimatabing, IV-V.1925, McGregor, Casiguran; Los Baños, P.I., Baker; Negros, IV-1911, C.V. Piper; Cuernos Mts., Negros, Baker; Island Polillo, Baker; Island Samar, Baker; Iligan and Davao, Mindanao, Baker.

Remarks. – This apparently common and widespread species is listed in Obenberger (1935) from Himalaya, Bengale and Japan as well as the Philippines. In the USNM collections, there are specimens from Laos, China and Taiwan as well. It may be distinguished from the other Philippine species

with its distinct elytral colour pattern shown in fig. 18 and as indicated in the key. The male genitalia are illustrated in fig. 19.

***Coroebus coelestis* Saunders**
(fig. 17)

Coroebus coelestis Saunders, 1874: 319. – Baer 1886: 126; Kerremans 1903: 233; Schultze 1916: 56; Obenberger 1935: 821.

Material. – Holotype, female (BMNH): Mindanao.

Remarks. – This large, subglabrous species may eventually need to be placed in a distinct genus, but this will await more detailed study of the entire complement of *Coroebus*. It is quite distinct from the other four species listed here as Philippine congeners and may be separated as in the key. The dorsal habitus is illustrated in fig. 17.

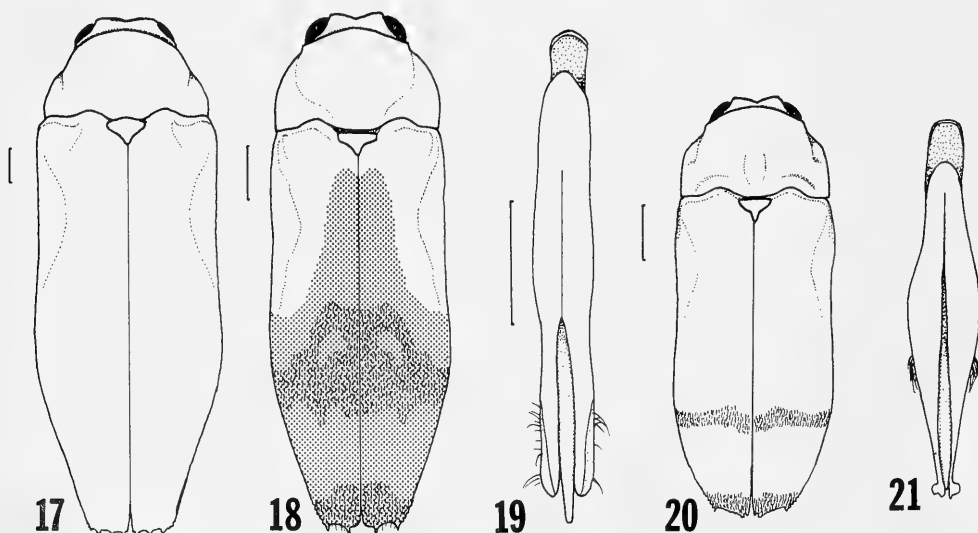
***Coroebus spinosus* (Fabricius)**
(figs. 20-21)

Buprestis spinosus Fabricius, 1801: 214.

Coroebus spinosus; Gory & Laporte 1839: 10; Baer 1886: 126; Kerremans 1903: 233; Schultze 1916: 56; Fisher 1921: 406; Obenberger 1935: 837.

Coroebus laportei Saunders, 1871: 104. – Baer 1886: 126; Obenberger 1935: 837.

Coroebus transversus Kerremans, 1900: 79. – Kerremans 1903: 232; Schultze 1916: 56; Théry 1927: 257; Obenberger 1935: 837.



Figs. 17-21. *Coroebus* spp., dorsal habitus and dorsal aspect of male genitalia. – 17, *C. coelestis*; 18, 19, *C. hastanus*; 20, 21, *C. spinosus* (scale lines = 1 mm, equal for figs. 19 and 21).

Material. – Of *transversus*, holotype, female (BMNH): Leyte; of *spinosus*, 5 examples (USNM): Mindanao, Dapitan and Davao.

Remarks. – The type of *spinosus* was unavailable for study and that of *laportei* was not borrowed. I have accepted the synonymy of previous authors, based on determined material in the USNM collection, comparison to the plates in Gory & Laporte (1839) and study of the type of *transversus*. This beautiful little species is quite distinct from the remainder of the Philippine species and may be separated by its coloration, vestiture and very different male genitalia as shown in figs. 20 and 21 respectively.

Coroebus albivestitus sp. n.
(figs. 22-24)

Type material. – Holotype, male (USNM): Philippines, Negros Or., Sibulan, Balingesay, 1981, C. K. Starr.

Description

Holotype, male. Size, 14.1×4.5 mm; elongate, subcylindrical, flattened above; dorsal integument colour nitid black with blue reflection, ventral colour subnitid black; head and pronotum sparsely covered with short, stout, recurved black setae except for slightly more dense patches of testaceous setae as follows: on head one pair dorsal to antennal cavities; on either side of pronotum dorsal to marginal carinae near apicolateral angle; elytra moderately setose with setae concentrated into patches and fasciae as in fig. 6; ventral surface partially covered with moderately dense recumbent testaceous setae, especially on hypomera, lateral thoracic sternites, metacoxal plate and first two abdominal sternites.

Head: with frontovertex longitudinally depressed between large eyes; inner margins of eyes diverging dorsally; circumocular groove extends along anterior margin from near dorsal apex of eye to before ventral apex; each antennal cavity bordered dorsally with one arcuate groove; supra-antennal grooves confluent with depressed base of frontoclypeus; frontoclypeus in shape of inverted 'Y', with apical margin angularly emarginate; area beneath each eye depressed for reception of basal antennomeres in repose; gena with acute angular projection; antennae with antennomere 2 longer than 3; 3 shorter than 4; 4-10 serrate, longer than wide; 11 shorter than 10, oblong.

Pronotum: slightly greater than $1.5\times$ as wide as long; widest at about middle; anterior margin strongly arcuate medially; posterior margin bisinuate on either side of truncate median portion

anterior to scutellum; basolateral angles obtuse, rounded; lateral margins carinate, finely crenulate, slightly diverging from base to about middle, then roundly arcuate to anterior margin; disc flattened, laterally convex, narrowly explanate before margins; scutellum large, subcordiform, longer than wide; basal margin truncate, lateral angles rounded, apex elongate, acuminate.

Elytra: slightly wider at base than pronotal base, widest at about apical third; humeri small, moderately elevated, oblique; lateral margins nearly straight from past base to basal third, then widening slightly to apical $1/3$ before narrowing to separately obliquely truncate apices, apices dentate as in fig. 6; pygidium slightly visible past elytra, broadly arcuate laterally, single short acuminate tooth medially.

Underside: suture between first two abdominal sternites feebly indicated laterally; premarginal groove extends along perimeter of sternite 5; femora subfusiform; tibiae flattened, subarcuate; tarsi short with claws bifid, inner teeth pointing inward. Genitalia: as in fig. 24, mounted on a point beneath specimen.

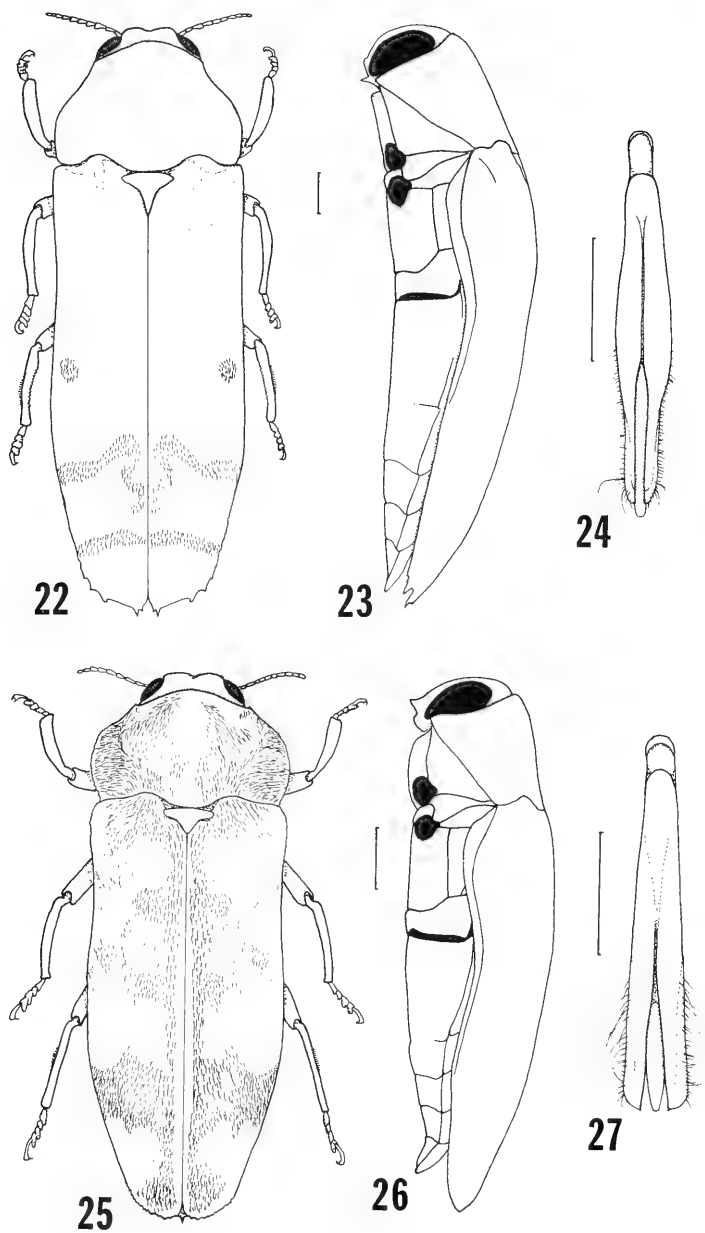
Remarks. – *Coroebus albivestitus* is named for the white setal vestiture of the elytra. This species is immediately distinguished from the remaining Philippine *Coroebus* spp. with its distinctive coloration, elytral setal pattern and male genitalia as illustrated and utilized in the key.

Coroebus bivestitus sp. n.
(figs. 25-27)

Type material. – Holotype, male (BPBM 14609): P. I., Negros Or. Nr. Mt. Talinas, 1020m, 27.VII.1958 / rain forest / H. E. Milliron collector.

Description

Holotype male. Size, 8.7×3.2 mm; elongate, subcylindrical, flattened above; dorsal integument colour subnitid black, with cupreous reflections lateral to pronotal gibbosity and along elytral suture, blue reflections in some lateral portions of elytra without dense setal covering; ventral colour subnitid black with slight aeneous reflections; head and pronotum moderately to densely covered with recumbent white and testaceous setae, more dense on ventral half of frontovertex and explanate portions of pronotum; elytra moderately setose with white setae concentrated into fasciae as in fig. 9 with testaceous setose longitudinal bands, which slightly expand into largest fascia past apical third; ventral surface generally covered with moderately dense recumbent off-white setae.



Figs. 22-27. *Coroebus* spp. – 22-24, *Coroebus albivestitus* sp. n.; 22, dorsal habitus; 23, left lateral aspect; 24, male genitalia, dorsal aspect; 25-27, *Coroebus bivestitus* sp. n.; 25, dorsal habitus; 26, left lateral aspect; 27, male genitalia, dorsal aspect (scale lines = 1 mm).

Head: with frontovertex longitudinally depressed between large eyes; a pair of feebly elevated small callous-like spots along eye margins near mid-point; inner margins of eyes subparallel, slightly diverging ventrally; circumocular groove extends along anterior margin from near dorsal apex of eye to before ventral apex; each antennal cavity bordered dorsally with one arcuate groove; frontoclypeus in shape of inverted 'Y', with apical margin arcuately emarginate; area beneath each eye depressed for reception of basal antennomeres in repose; gena with acute angular projection; antennae with antennomere 2 slightly longer, wider than 3; 3 and 4 subequal; 5-10 serrate, longer than wide; 11 subequal to 10, oblong.

Pronotum: $1.7\times$ as wide as long; widest at about middle; anterior margin moderately arcuate; posterior margin bisinuate on either side of truncate median portion anterior to scutellum; basolateral angles obtuse; lateral margins carinate, crenulate, broadly arcuate from base to apex; disc convex, lateral and basolateral areas explanate before margins; scutellum subcordiform; basal margin subtruncate, lateral angles rounded, apex elongate, acuminate.

Elytra: slightly wider at base than pronotal base, widest at about apical $1/3$; humeri small, moderately elevated, oblique; lateral margins entirely finely serrate, nearly straight from past base to basal $1/3$, then widening slightly to apical $1/3$ before narrowing to separately rounded apices; pygidium not visible past elytra.

Underside: suture between first two abdominal sternites feebly indicated laterally; premarginal groove extends along perimeter of sternite 5; femora subfusiform; tibiae flattened, subarcuate; tarsi short with claws appendiculate.

Genitalia: as in fig. 27, mounted on point beneath specimen.

Remarks. – *Coroebus bivestitus* may be separated from its congeners with its bicolorous elytral setal pattern and the male genitalia as illustrated in figs. 25 and 27 respectively. The species is named for the bicolored elytral setae.

Incertae sedis

Coroebus bajulus Deyrolle

Coroebus bajulus Deyrolle, 1864: 122. – Baer 1886: 126; Kerremans 1903: 232; Fisher 1921: 406; Obenberger 1935: 820.

Remarks. – Saunders (1874) stated that he thought that this species would prove to be a variety of *bastanus*. Although Fisher (1921) listed this species from Negros and Obenberger (1935) also

listed Luzon, I do not believe that this species really exists within the Philippine fauna. The two specimens that Fisher recorded are preserved (USNM) within a larger series from several different Philippine localities and labelled in his hand as *C. bastanus*; these locality data are listed otherwise irregularly under that species. *C. bajulus* was described from Ceram and there are very few known distributional tracks corroborated by buprestids between this part of Indonesia and the Philippines.

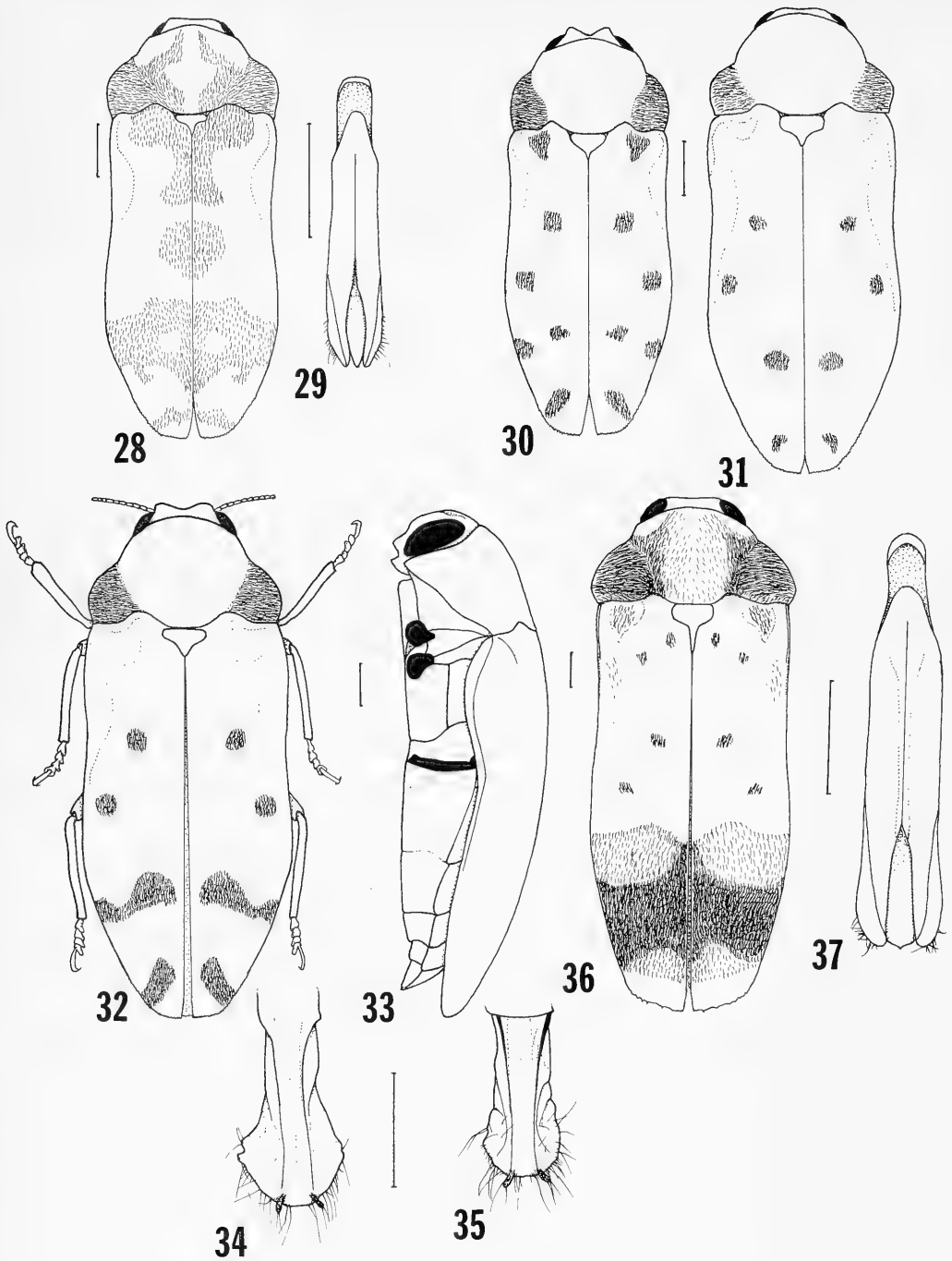
Genus *Cisseicoraebus* Kerremans

Cisseicoraebus Kerremans, 1903: 253; Schultze 1916: 56; Fisher 1921: 350; Obenberger 1935: 814; Bellamy 1985: 425; 1990: 691. – Type-species: *Coroebus grandis* Kerremans [here designated].

Remarks. – At the time the genus was described, Kerremans (1903) listed three species, *C. grandis* (Kerremans) from Samar, *C. retrolatus* (Deyrolle) from Indonesia and *C. subcornutus* (Fairmaire) from Gabon, with the latter now placed in the genus *Euchroaria* Obenberger. As Kerremans was generally not in the habit of designating generic type species, and I can find no indication that such has been done for *Cisseicoraebus*, I designate *grandis* as the type species for this taxon.

Key to the Philippine species of *Cisseicoraebus*

1. Dorsal surface black with setae white and distributed on elytra in small patches and broad fasciae (e.g. figs. 28, 36) 2
- Dorsal surface with pronotum green or cupreous and elytra green; setae golden and distributed on elytra in patches and narrow fasciae 3
2. Lateral areas of pronotum and apical $1/2$ of elytra densely covered with elongate yellowish white setae; basal $1/2$ of each elytron with six setal patches; elytral apices with more elongate slightly recurved denticles; membraneous lobes of parameres more expanded (fig. 37) (Samar) *C. grandis* (Kerremans)
- Lateral areas of pronotum and elytra with a more sparse covering of elongate white setae; both base of elytra and broad fascia from about apical $1/3$ to apical $1/6$ setose, elytral disc otherwise setose as in fig. 28; elytral apices serrate; membraneous lobes of parameres narrow (fig. 29) (Luzon) *C. pullatus* (Saunders)
3. Dorsal surface unicolorous, dark green; each elytron with four round and two elongate setal patches, one elongate patch in basal depression (Lamao, Luzon) *C. piperi* (Fisher)
- Dorsal surface bicolorous, head and pronotum differing in colour from elytra; no setal patch



Figs. 28-37. *Cisseicoraebus* spp., dorsal habitus, male and female genitalia, dorsal aspect. – 28, 29, *C. pullatus*; 30, 35, *C. piperi*; 31, *C. cisaeoides*; 32-34, *Cisseicoraebus bicoloratus* sp. n.; 33, left lateral aspect; 36, 37, *C. grandis* (scale lines = 1 mm).

- in basal elytral depression 4
4. Head and pronotum with cupreous reflection, especially pronotal base; each elytron with five more or less round setal patches (Mindanao) *C. cisseoides* (Saunders)
- Head and pronotum roseocupreous; each elytron with two round setal patches on disc and two elongate, partially oblique, fasciae on apical 1/3 (Mt. Maquiling, Luzon) *C. bicoloratus* sp. n.

***Cisseicoraebus grandis* (Kerremans)**

(figs. 5-8, 14, 36-37)

Coroebus grandis Kerremans 1900: 77.*Cisseicoraebus grandis*; Kerremans 1903: 253; Schultze 1916: 56; Fisher 1926: 242; Obenberger 1935: 814.

Material. – 2 examples (USNM): Island Samar, Baker.

Remarks. – This large, attractive species is most similar to *C. retrolatus* from Sumatra and Borneo. I have not seen an example of *retrolatus* and, thus, cannot diagnose the differences of these two taxa. Of the Philippine species, *grandis* is distinctive in its size and pattern of vestiture and may be separated as indicated in the key and as illustrated.

***Cisseicoraebus pullatus* (Saunders) comb. n.**

(figs. 28-29)

Coroebus pullatus Saunders, 1874: 320. – Baer 1886: 126; Kerremans 1903: 223; Schultze 1916: 56; Obenberger 1935: 832.

Material. – Holotype, male (BMNH): Luzon.

Remarks. – This species is similar in habitus to *C. opaculus* Obenberger described from India, but I have not been able to compare them directly, so cannot comment on specific differences. At the time this species was described, Saunders (1874) stated that it was 'most like *retrolatus*, H. Deyr., of any species I know, which it should follow'. Obenberger (1935) listed *retrolatus* under *Cisseicoraebus*. Within the Philippine fauna, *pullatus* is immediately distinguished by its coloration, vestiture and male genitalia as indicated in the key and shown in figs. 28 and 29.

***Cisseicoraebus piperi* (Fisher) comb. n.**

(figs. 30, 35)

Coroebus piperi Fisher, 1921: 406. – Obenberger 1935: 832.

Material. – Holotype, female (USNM 51490): Lamao, Luzon, P.I., III-VI, 1911, C. V. Piper, collector.

Remarks. – This and the following two species are apparently closely related by virtue of a very similar set of integument coloration and the setal patterns of the pronotum and elytra. With no males known for any of the three species, I have illustrated the ovipositors to distinguish *C. piperi* (fig. 35) from *C. bicoloratus* (fig. 34). These three species are separated as indicated in the key and by the specific patterns of the elytral setal patterns shown in figs. 30, 31 and 32 respectively.

***Cisseicoraebus cisseoides* (Saunders) comb. n.**

(fig. 31)

Coroebus cisseoides Saunders, 1874: 319. – Baer 1886: 126; Kerremans 1903: 233; Schultze 1916: 56; Obenberger 1935: 821.

Material. – Holotype, female (BMNH): East Mindanao; 1 ex. (NSMT): Agusan d. N., Mindanao, V.1977.

Remarks. – At first glance, *C. cisseoides* appears to be a transitional form between *piperi* and *bicoloratus*, however the absence of both males and specimens other than the types makes it difficult to comment further on the relationship of these three species. It may be separated from its congeners as indicated in the key and as discussed previously.

***Cisseicoraebus bicoloratus* sp. n.**

(figs. 32-34)

Type material. – Holotype, female (USNM): Mt. Makiling, Laguna, P.I., v.9.31 / F. C. Hadden collector; 1 paratype, female (NMPC): Mt. Maquiling, elev. 1800 m, 24.v.1949, P. Namocale.

Description

Holotype, female. Size, 12.2 mm × 5.0 mm; elongate, ovoid, flattened above and below; head and pronotum dark cupreous with reddish tinge; elytra bluish green; ventral surface, legs and antennae aeneous; dorsal surface moderately densely covered with medium-sized shallow punctures, elytra otherwise subrugose; ventral surface sparsely punctate medially, subimbricate laterally; dorsal surface generally with a single short silver recumbent seta from each puncture, otherwise with dense concentrations of recumbent yellow setae on frontal depression between eyes, flattened lateral areas of pronotum and in patches and fasciae on elytra as in fig. 32; ventral surface very sparsely setose medially, much more densely covered with long recumbent yellow setae on hypomera and lateral thoracic and abdominal sternites.

Head: frontovertex with lateral lobes produced between eyes, longitudinally depressed medially;

eyes large, ovoid, with ventral margin truncate dorsal to genal antennal groove, inner margins subparallel; circumocular groove only along inner margins; one small arcuate supraantennal groove with a slight dorsal gibbosity above each antennal insertion; frontoclypeus compressed between large antennal cavities, distal emargination moderately shallow, subtriangular; gena lobe with acute projection. Antennae with antennomere 2 subequal to 1, widest distally; 3 shorter than 2; 4-10 triangularly serrate; 11 oblong, curved.

Pronotum: $1.66\times$ as wide as long, widest near middle; anterior margin arcuate; posterior margin biarcuate on either side of subtruncate prescutellar median lobe; posterolateral angles subacute; lateral margins broadly arcuate from base to apex, crenulate; disc strongly convex between strongly explanate lateral portions. Scutellum large, broadly cordiform.

Elytra: wider than pronotum posterior to humeri, widest at about apical third; lateral margins biarcuate before gradually narrowing to subtruncate apex; margin crenulate to about apical third then serrulate to apex; premarginally deeply impressed along basal third; disc transversely convex laterally, flattened medially; one basomedial depression on either elytron; epipleuron broadest basally then gradually narrowing along entire length.

Underside: prosternum ventrally produced, anterior margin subtruncate medially, arcuate laterally with emargination for antennae in repose; process slightly swollen posterior to procoxae then attenuate to rounded apex; metepisternum with inner margin strongly arcuate; metacoxal plate with posterior margin slightly dilated, evenly transverse; sutures between abdominal sternites transverse medially, arcuate laterally; sternite 1 nearly $2\times$ length of 2; $1 + 2$ longer than $3 + 4 + 5$; 2-5 with groove between pleurite border and disc; 5 broadly arcuate; legs: femora narrow, subfusiform; protibiae flattened, meso- and metatibiae subcylindrical; tibiae armed with two short distal spines; tarsomeres 1-4 subequal, each slightly shorter than preceding and with slightly more expanded ventral pulvillus; 5 narrow, elongate, claws stout, bifid, inner teeth broad, shorter than outer teeth. Ovipositor: as illustrated in fig. 34, mounted on point beneath specimen.

Variation. Size, $12.1\text{ mm} \times 4.8\text{ mm}$. The single female paratype is virtually identical to the holotype in all aspects of coloration, vestiture and sculpture.

Remarks. – This species is named for its bicolorous dorsal integument. It comes nearest to *C. cis-seoides* and may be distinguished as indicated under that species and in the key above.

Genus *Philocoroebus* gen. nov.

Type-species: *Coroebus azureipennis* Obenberger [new designation].

Short, ovoid, subcylindrical, convex above, flattened below. Head produced, bilobed between eyes; eyes large, inner margins diverging dorsally; frontal disc entire; supraantennal transverse groove entire; antennal cavities large; frontoclypeus compressed between antennae, distal margin emarginate; gena lobate. Antennae serrate from antennomere 5. Pronotum wider than long; disc convex, somewhat gibbose; lateral portions explanate, margins carinate; with one short prelateral carina on each side. Scutellum large, triangular or cordiform.

Elytra convex, subparallel, attenuate to separately rounded or angulate apices; epipleuron separated from disc by carina, extending to well beyond middle. Thoracic sternites. Prosternum short, longitudinally convex, mentonierre entire, short, feebly produced; process with sides subparallel to rounded apex. Mesepisternum, mesepimeron elongate, oblique. Metepisternum narrow, elongate. Metepimeron not visible. Metacoxa short, broad, feebly dilated distally.

Abdominal sternites. Suture between sternites 1 and 2 feebly indicated, somewhat concave anteriorly; sutures between sternites 2, 3, 4 and 5 evenly transverse.

Legs. Femora narrowly fusiform. Tibiae elongate, with pair of distal spines; metatibia with setal comb on external edge. Tarsi short, tarsomeres 1-4 subequal, each with ventral pulvillus; 5 narrow, elongate, claws appendiculate.

Wing as in figs. 15, 16; radial sector vein extending basally about same distance as median vein; radiomedial crossvein extends from posterior angle of radial cell; some branches of anal veins poorly indicated.

Genitalia: male aedeagus short, parameres partially fused basally, some with various apical membranous modifications as shown figs. 42, 44, 46, 48, 50, 52 and 54; ovipositor of 'normal type'.

Remarks. – The generic name is a combination of the prefix from Philippines mated with the nominate generic epithet for this large buprestid tribe. The name was chosen to reflect the fact that this group of species is apparently restricted to various islands in the Philippine archipelago.

Fisher (1921) recognized two groups of species in his discussion and key for *Coroebus* [sic] but did nothing further to separate them. The character state of the pronotal prelateral carina is not absolute as some of the species do not exhibit the presence of this state. The loss of the prelateral

carina is felt to be a character state reversal as the other aspects of the morphology of these congeners agree in the perceived characters of importance. *Philocoroebus* can be separated from the other members of the tribe as indicated in the generic key above and the species are distinguished below.

Key to the species of *Philocoroebus*

1. Pronotum with prelatelateral carinae, one on either side (e.g. figs. 38, 39) 2
- Pronotum without prelatelateral carinae (i.e. figs. 45, 51, 56) 9
2. Body more ovoid, $L/W \leq 2.35$ 3
- Body more elongate, $L/W \geq 2.50$ 6
3. Elytra with transverse setal fasciae
..... *P. azureipennis* (Obenberger)
- Elytra without setae concentrated into transverse fasciae 4
4. Dorsal surface colour black with pronotum reflecting blue-green, elytra reflecting deep blue; male genitalia with parameres subparallel and with projecting membranous lobes apically (fig. 48) (Samar) *P. samarensis* sp. n.
- Dorsal surface iridescent blue or blue green; parameres strongly diverging apically, some part of each apex membranous, but without projecting lobe (e.g. fig. 42) 5
5. Dorsal integument deep blue; male genitalia as in fig. 42 (Luzon)
..... *P. banahaoensis* (Obenberger)
- Dorsal integument blue-green to deep blue; male genitalia as in fig. 44 (Luzon)
..... *P. maquilingensis* sp. n.
6. Dorsal integument iridescent green with or without blue reflection 7
- Dorsal integument iridescent deep blue with either green or purple reflections 8
7. Elytra with transverse setal fasciae; ventral surface black with slight iridescent reflections (Luzon) *P. elongatus* sp. n.
- Elytra without setae concentrated into transverse fasciae; ventral surface iridescent green (Luzon) *P. meliboeiformis* (Saunders)
8. Prosternum with process more narrow in proportion to entire length (PS L/W 2.50) (Luzon) *P. alius* sp. n.
- Prosternum broader (PS L/W 2.11) (Mindanao) *P. adamantinus* sp. n.
9. Pronotum with lateral explanate areas covered with recumbent setae; elytra with small setal patches resembling some spp. of *Cisseis* (Luzon) *P. pseudocisseis* sp. n.
- Dorsal surface without any concentrations of setae as above 10
10. Dorsal surface iridescent green with blue reflections (Luzon) *P. cyaneoviridis* (Fisher)
- Dorsal surface colour deep iridescent purple

(Luzon) *P. purpureus* sp. n.

Philocoroebus azureipennis (Obenberger)

comb. n. (figs. 9-12, 15, 38-40)

Coroebus azureus Fisher, 1921: 405 [name preoccupied]
Coroebus azureipennis Obenberger, 1935: 820 [new name]

Material. – Holotype, female (USNM 51489): Baguio, Benguet, Luzon, Baker; 8 females (3 USNM, 3 BPBM, 2 CLBC) Mt. Makiling, Laguna, Luzon, P. I., various dates IV-VI.1931 / 1932, F. C. Hadden; 1 female (USNM), Agr. College, Laguna, P. I., V.19.[19]31 / F. C. Hadden.

Description

The original description of Fisher (1921) is more than adequate and only the following diagnostic comments are given to allow a confident definition of this species in comparison to the many new ones described below.

Diagnosis. Holotype, female. Size, 7.3×2.9 mm; ovoid, transversely convex above; shining blue green iridescence dorsally; black ventrally; surface generally imbricate; dorsal surface sparsely covered with recumbent grey setae, slightly more dense, regular on elytra; elytral fasciae with white setae as in fig. 38; ventral surface more densely covered with adpressed white setae. Head longitudinally depressed from vertex along entire length of frons; supraantennal grooves strongly arcuate, moderately wide; antennal cavities separated by width subequal to each repective width; distal margin of frontoclypeus emarginate, straight medially, angulate laterally. Pronotum nearly $1.8 \times$ wide as long; with prelatelateral carinae. Prosternum $2.0 \times$ as long as wide. Ovipositor as illustrated in fig. 40. Variation ($n = 10$). Size: length, $5.8-7.3$; width, $2.4-2.9$ mm; the dorsal coloration varies from steel blue with a slight purple reflection to a deep metallic green without any blue tinge visible.

Male: unknown.

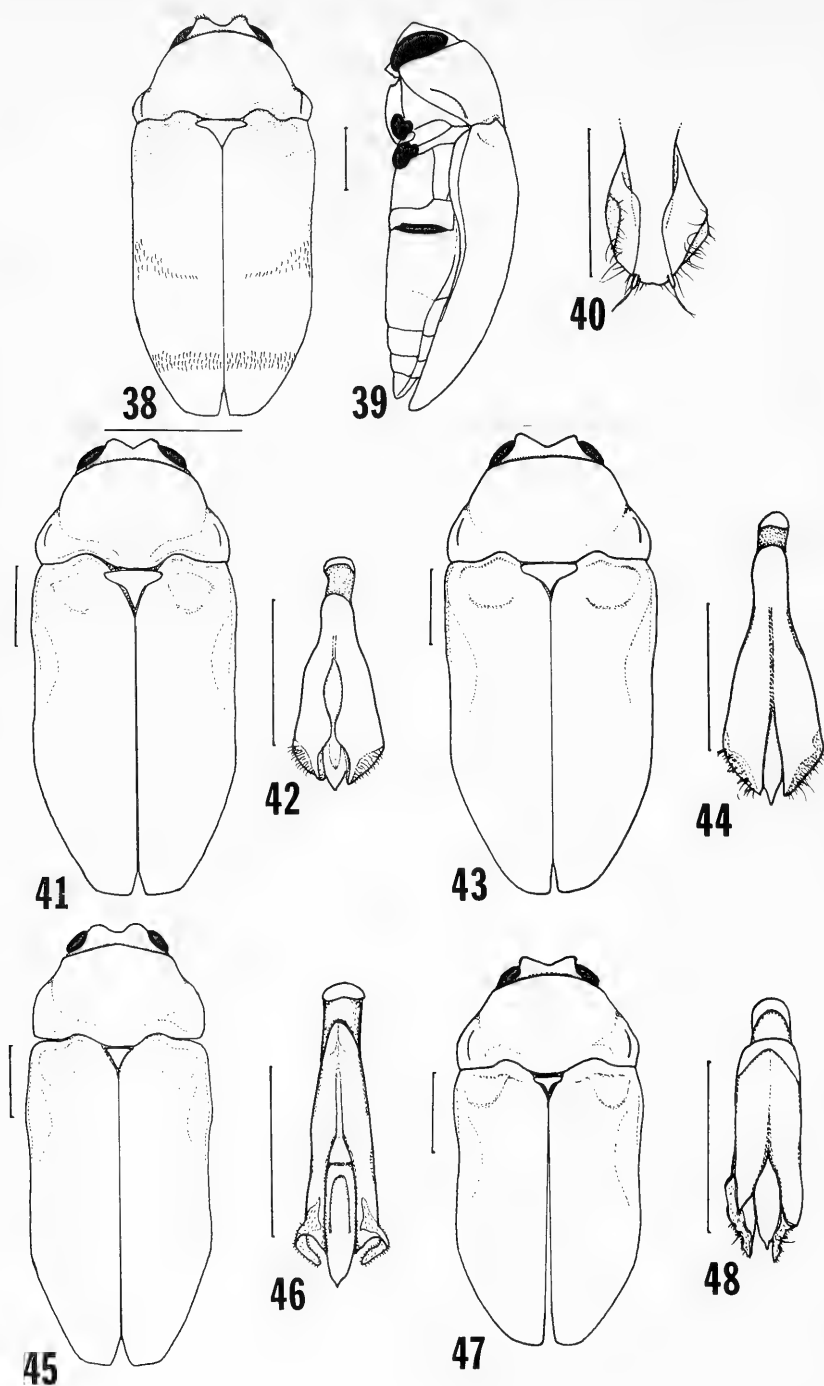
Remarks. – This species may only possibly be confused with *P. elongatus* sp. n. due to the similar dorsal coloration and vestiture, however the body proportions and more complex development of the elytral setae pattern of *elongatus* will immediately separate these two taxa.

Philocoroebus banahaoensis (Obenberger)

comb. n. (figs. 41, 42)

Coroebus banahaoensis Obenberger, 1928: 338. – Obenberger 1935: 820.

Material. – Lectotype, male [new designation] (NMPC 23709): Mt. Banahao, Luzon, G. Boettcher leg.; 1 male



Figs. 38-48. *Philocoroebus* spp., dorsal and lateral habitus, male and female genitalia. - 38-40, *P. azureipennis*; 41, 42, *P. babanaoensis*; 43, 44, *P. maquilingensis* sp. n.; 45, 46, *P. purpureus*; 47, 48, *P. samarensis* (scale lines = 1 mm).

paralectotype (NMPC 23710): same data; 1 male (USNM), Mt. Banahao, P.I., Baker.

Description

The original description of two syntypes by Obenberger (1928) is sufficient to warrant just the following diagnosis.

Diagnosis. Lectotype, male. Size, 5.5×2.4 mm; ovoid; convex above; flattened below; dorsal surface iridescent greenish blue with moderate purple tinge on elytra; entire surface imbricate; dorsal surface sparsely covered with recumbent grey setae, slightly more dense, regular on elytra; ventral surface more densely covered with adpressed white setae. Head longitudinally depressed; supraantennal grooves strongly arcuate, wide; antennal cavities separated by distance subequal to their individual widths; frontoclypeus arcuately emarginate distally. Pronotum nearly $1.9\times$ as wide as long, with prelateral carinae; Prosternum nearly $2.3\times$ as long as wide. Genitalia: as in fig. 42, mounted on point with specimen.

Variation ($n = 3$). Size: length, 5.5-5.7; width, 2.4-2.9 mm; the dorsal colour varies in both the paralectotype and the only other specimen on hand by both having the purple tint lost completely and thus being mostly steel blue on the elytra.

Female: unknown.

Remarks. – This species is quite similar to *P. maquilingensis* sp. n. and other than the differences in the male genitalia, I would have probably left them together. They are separated as indicated in the key and mostly on the basis of the shape and proportional differences of the male genitalia. As there is overlap between these two mountains in both types series, there is undoubtedly some type of ecological allopatry involved which can explain this divergence.

Philocoroebus maquilingensis sp. n. (figs. 43, 44)

Type material. – Holotype, male (USNM): Mt. Makiling, Luzon, Baker; 3 male paratypes: 1 (BPBM), same data as holotype except VI.1.[19]32 / F. C. Hadden collector; 1 (USNM), Lamao, Luzon, III-VI.(19)11 P I / CV Piper Collector; 1 (USNM), Mt. Banahao, P.I., Baker.

Description

Holotype, male. Size: 6.7×2.6 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent bluish green, ventral surface black with strong blue green reflection; head black with blue and purple reflections; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugu-

lose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with more dense covering of more elongate, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus broadly arcuately emarginate; supraantennal grooves strongly arcuate, relatively broad; antennal cavities separated by distance much less than their separate width. Pronotum nearly $1.9\times$ wide as long; short, prelateral carinae feebly indicated. Elytra with lateral carina serrulate; epipleuron extends to apicolateral angle. Prosternum slightly more than $2.4\times$ long as wide; with widely separated, feebly produced, bilobed mentonierre. Genitalia: as in fig. 44, mounted on point with specimen. Variation ($n = 4$). Size: length, 5.8-6.1; width, 2.4-2.8 mm; the colour of one paratype is a much deeper blue with no trace of green.

Female: unknown.

Remarks. – *Philocoroebus maquilingensis* comes nearest to *P. banahaoensis* and is distinguished from that species by the differences in coloration, vestiture and the male genitalia. These two species are also close to the next new species, *P. samarensis*. These species can be separated as indicated in the preceding key.

Philocoroebus samarensis sp. n. (figs. 47, 48)

Type material. – Holotype, male (USNM): Island Samar, Baker.

Description

Holotype, male. Size: 4.8×2.2 mm; elongate ovoid, convex above, flattened below; dorsal and ventral surfaces shining black with faint blue and purple reflections; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with moderate covering of short, fine, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves arcuate, narrow; antennal cavities separated by a distance equal to their separate width. Pronotum $1.9\times$ as wide as long; with prelateral carinae. Elytra with lateral carinae finely serrate. Prosternum $1.8\times$ as long as wide. Genitalia: as in fig. 48, mounted on point with specimen.

Female: unknown.

Remarks. – This species is unique in that it is both the smallest species and specimen of *Philocoroebus*, is entirely black and is the only specimen known from the island of Samar, hence the name. The aedeagus is very different from the other two species of the perceived species-group, *P. banaobaoensis* and *P. maquilangensis* and will serve to immediately distinguish *P. samarensis* from its congeners.

***Philocoroebus meliboeiformis* (Saunders)**
comb. n. (figs. 49, 50)

Coroebus meliboeiformis Saunders, 1874: 321. – Baer 1886: 126; Kerremans 1903: 233; Schultze 1916: 56; Fisher 1921: 406; Obenberger 1935: 831.

Material. – Holotype, male (BMNH): C. Luzon.

Description

Holotype, male. Size: 7.3 mm \times 3.0 mm; elongate ovoid; convex above, flattened below; shining golden green above and below, except for apical half of elytra which is black; surface generally imbricate, with elytral disc rugose; moderately covered with short, recumbent white setae. Pronotum 1.6 \times as wide as long; pronotum with prelateral carinae. Prosternum 2.2 \times as long as wide. Genitalia: as in fig. 50, mounted on card with specimen.

Female: unknown.

Remarks. – This is the only species of *Philocoroebus* which is brightly coloured on the ventral surface. The holotype is somewhat damaged as it was originally prepared with a very oversized pin; it is now mounted on a card along with the genitalia and the right middle leg.

***Philocoroebus cyaneoviridis* (Fisher) comb. n.**
(figs. 51, 52)

Coroebus cyaneoviridis Fisher, 1922: 14. – Obenberger 1935: 822.

Material. – Holotype, male (USNM 24670): Baguio, Luzon, Philippine Islands.

Description

Fisher's (1922) original description is quite informative, so the following diagnosis is provided solely for comparison.

Diagnosis. Holotype, male. Size: 6.9 \times 2.7 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent green with some lateral and apical blue reflections, epipleuron black with pur-

plish blue reflections, ventral surface black; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with moderate covering of short, fine, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves arcuate, narrow; antennal cavities separated by a distance equal to their separate width. Pronotum nearly 1.9 \times as wide as long, without prelateral carinae. Elytra with lateral carinae finely serrulate on basal 2/3, serrate to apicolateral angle, then finely dentate; apices separately angulately truncate. Prosternum 2.2 \times as long as wide. Genitalia: as shown in fig. 52, mounted on point with specimen.

Female: unknown.

Remarks. – This species and the following are very close in many character states and differ from the remaining congeners in that they are two of three which lack the prelateral carinae. The general morphology is very similar with only the coloration of the dorsal integument significantly different. The male genitalia are very similar yet differ in the details of the projecting membranous lobes. These two species may be separated with their differing coloration.

***Philocoroebus purpureus* sp. n.**
(figs. 45, 46)

Type material. – Holotype, male (USNM): Mt. Makiling, Laguna, P.I., V.6.[19]31 / F. C. Hadden collector.

Description

Holotype, male. Size: 6.2 \times 2.4 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent purple with some lateral blue reflections, epipleuron and ventral surface black; head black with blue green reflections; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with moderate covering of short, fine, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves arcuate, narrow; antennal cavities separated by a distance equal to their separate width. Pronotum slightly more than 1.8 \times as wide as long, without prelateral carinae. Elytra with lateral carinae denticulate; apices separately

angulately truncate. Prosternum $2.0\times$ as long as wide. Genitalia: as in fig. 46, mounted on point beneath specimen.

Female: unknown.

Remarks. – The specific epithet is obviously coined for the distinctive dorsal coloration. *P. purpureus* was discussed above in comparison to *P. cyaneoviridis*.

***Philocoroebus alius* sp. n.**

(figs. 16, 53–54)

Type material. – Holotype, male (USNM): Majajay, Laguna, Mar. 6, (19)28, Luzon, P.I. / Colln R. C. McGreggor.

Description

Holotype, male. Size: 7.8×3.1 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent blue green with some laterobasal golden reflections on the pronotum, ventral surface black; head black with blue green reflections on vertex and roseocupreus reflections on frons; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with moderate covering of short, fine, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves arcuate, narrow; antennal cavities separated by a distance slightly greater than their separate width. Pronotum nearly $1.7\times$ as wide as long; with prelateral carinae. Elytra with marginal carinae finely serrulate to apicolateral angle, then finely dentate along rounded apical margin. Prosternum $2.5\times$ as long as wide. Genitalia: as in fig. 54, mounted on point with specimen. Wing: as in fig. 16.

Female: unknown.

Remarks. – *Philocoroebus alius* comes nearest to *P. adamantinus* n. sp. and may be separated as indicated in the key above. These species differ in the colour of the dorsal integument, vestiture, the amount of projection of the frontovertex between the eyes, shape of frontoclypeal emargination and in the two type localities, each from one of the two largest and widely separated Philippine islands. The specific name comes from the Latin, meaning 'another'.

***Philocoroebus adamantinus* sp. n.**

(fig. 55)

Type material. – Holotype, female (USNM): Butuan, Mindanao, Baker.

Description

Holotype, female. Size: 6.8×2.7 mm; elongate ovoid, convex above, flattened below; dorsal surface nitid black with blue reflections on pronotum and elytra and purple reflections on humeri, epipleuron and ventral surface black; head black with blue and golden green reflections; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; ventral surface with moderate covering of short, fine, adpressed, white setae. Head with broad longitudinal depression from vertex along entire length of frons; clypeus emarginate; supraantennal grooves evenly transverse medially, arcuate laterally, narrow; antennal cavities separated by a distance slightly greater than their individual width. Pronotum slightly more than $1.7\times$ as wide as long; with prelateral carinae. Elytra with marginal carinae finely serrulate along basal $2/3$, slightly more so on attenuate apical third, but less so on narrow, separately rounded apices. Prosternum $2.3\times$ as long as wide.

Male: unknown.

Remarks. – The specific epithet is from the Latin, meaning "steel blue". This species comes nearest *P. alius* as discussed above.

***Philocoroebus elongatus* sp. n.**

(figs. 58, 59)

Type material. – Holotype, female (USNM): Majajay, Mar. 30, [19]29, Lagun, Luzon, P. I. / Colln R C McGreggor; 3 female paratypes (BPBM): 1, P. I. Luzon, Camarines Sur, Mt. Isarug, Pili, 800m, 27.IV.1965 / H. M. Torrevillas collector; 1, Ifugao Prov., Liwo, 8 km E Jayoyao, 1000–1300m, 30.V.1967 / L. M. Torrevillas collector; 1, same except Jacmal Bunhian, 24 km E Mayoyao, 800–1000m, 27–29.IV.1967 / H. M. Torrevillas, light trap.

Other material. – 3 specimens (NSMT): C. Luzon, Mountain Prov., 3.VII.1989.

Description

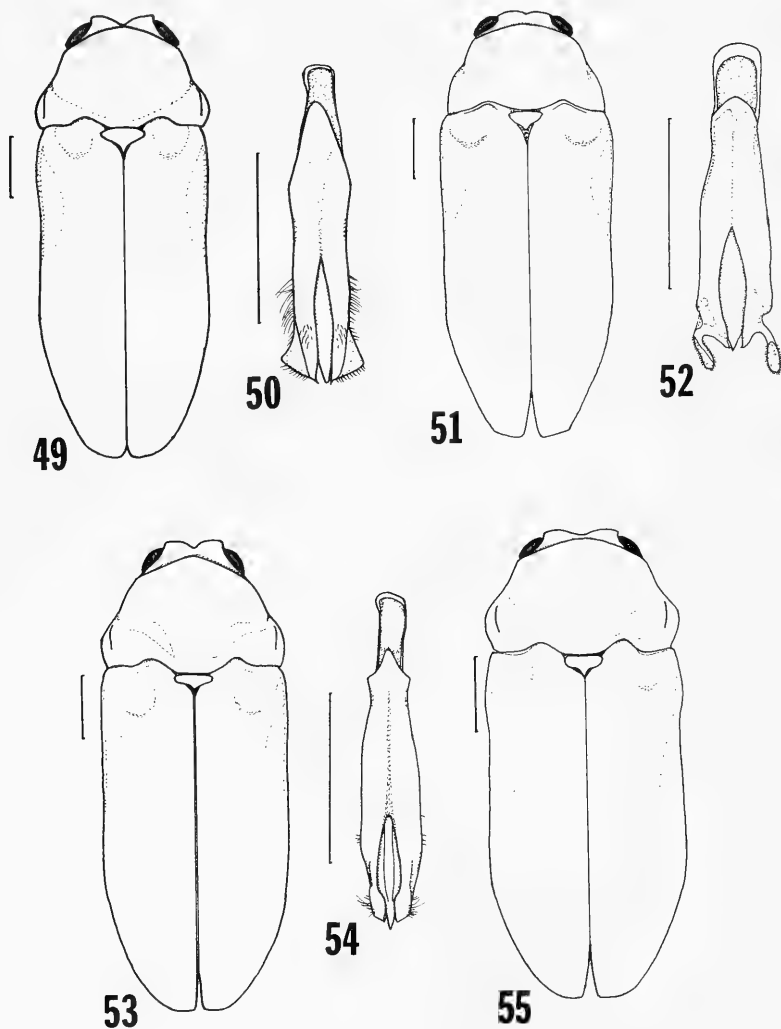
Holotype, female. Size: 7.7×3.0 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent blue green, ventral surface black; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with elongate, recumbent grey setae; elytra with elongate, recumbent white setae concentrated into patches and

fasciae as in fig. 58; ventral surface with moderate covering of short, fine, adpressed, white setae. Head bilobed, strongly produced anteriorly between eyes, longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves strongly arcuate, wide; antennal cavities separated by a distance subequal to their separate width. Pronotum nearly 1.8× as wide as long; with prelateral carinae. Elytra with marginal carinae finely serrulate to apicolateral angle, then finely dentate along rounded apical margin. Prosternum 2.3× as long as wide. Variation (n = 4). In size, 7.7-8.3 × 2.9-3.4 mm; the three

paratypes are more strongly green than blue green in the dorsal coloration.

Male: unknown.

Remarks. – *Philocoroebus elongatus* is named for being the most elongate member of the new genus. Due to the pubescent patches and fasciae, it may be confused with both *P. azureipennis* and *P. pseudocisseis* n. sp. but may be separated from either of these as indicated in the key. *P. azureipennis* is much shorter in proportion and differs in the distribution of the elytral setal patches, while *P. pseudocisseis* lacks the prelateral pronotal carinae



Figs. 49-55, *Philocoroebus* spp., dorsal habitus and male genitalia. – 49, 50, *P. meliboeiformis*; 51, 52, *P. cyaneoviridis*; 53, 54, *P. alius* sp. n.; 55, *P. adamantinus* sp. n. (scale lines = 1 mm).

and has the elytral setae concentrated only in patches, lacking the apical fascia.

The three specimens from Mountain Prov., C. Luzon are an apparent variant of this species. They differ by being consistently larger and the colour is more of a brassy green. Without males present, I prefer to neither make these three paratypes nor to consider them as another new taxon.

Philocoroebus pseudocisseis sp. n.
(figs. 56, 57)

Type material. – Holotype, female (USNM): Mt. Makiling, Laguna, P. I. IV.21.[19]31 / F. C. Hadden collector; 3 female paratypes: 1 (USNM), same data as holotype; 1 (USNM), same data except V.6.[19]31; 1 (BPBM): same data except IV.19.[19]31 / elevation 3000 ft. / flowers of malaklak.

Description

Holotype, female. Size: 6.9×2.8 mm; elongate ovoid, convex above, flattened below; dorsal surface iridescent golden green, epipleuron and ventral surface black; pronotum and medial parts of ventrites imbricate, punctate; lateral portion of abdominal sternite 1 longitudinally rugulose; elytra rugose; dorsal surface generally moderately covered with fine, short, recurved testaceous setae; elytra with elongate, recumbent, stout, white setae concentrated into small patches distributed on disc as in fig. 56; ventral surface with moderate covering of short, fine, adpressed, white setae. Head longitudinally grooved from vertex along entire length of frons; clypeus convexly emarginate; supraantennal grooves strongly separately arcuate, wide; antennal cavities separated by a distance slightly greater than their individual width. Pronotum $1.8\times$ as wide as long; lateral area explanate with moderately dense covering of transversely recumbent yellowish white setae; without prelateral carinae. Elytra with marginal carinae finely serrulate on attenuate apical third, more finely dentate on apicolateral angle, then entire along separately subtruncate apices. Prosternum slightly more than $2.2\times$ as long as wide. Genitalia: (not illustrated) mounted on a point beneath specimen. Variation ($n = 4$). In size, $6.9\ 7.9 \times 2.8\ 3.0$ mm; the coloration is fairly constant except for some blue green elytral reflections on the largest paratype.

Male: unknown.

Remarks. – This species is named for its similar appearance to numerous species of the Australasian genus *Cisseis* but can be separated from that taxon as in the generic key. As discussed above under *P. elongatus*, *P. pseudocisseis* comes near both that species and *P. azureipennis* is general

appearance but differs considerably. These three species may be separated as discussed previously and as in the species key above.

Genus *Cisseis* Gory & Laporte

Cisseis Gory & Laporte, 1839: 1. – Kerremans 1893: 117; 1903: 227; Obenberger 1935: 842; Bellamy 1985: 425.
– Type-species: apparently not yet designated (see discussion below).

Remarks. – In his revision of the Australian species of *Cisseis*, Carter (1923) briefly discussed the original generic description and the six species assigned by Gory & Laporte (1839). There was no designation in that work of a type-species and I am unaware of any subsequent designation; this should be left to the eventual, and long overdue, new revision of this largest generic component of the Australian Coroebini.

Cisseis aquilonia sp. n.
(figs. 60-62)

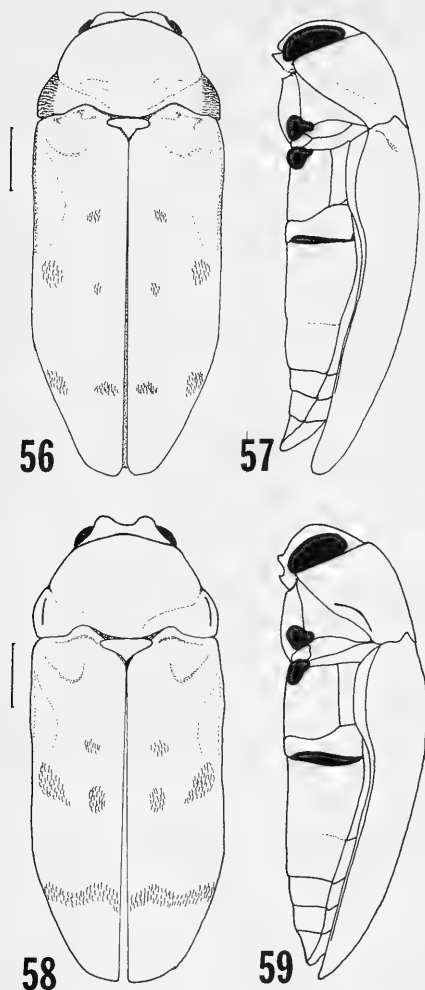
Type material. – Holotype, male (BPBM 14607): Philippine Is., Sur, Iriga Camarines, VII.2-14-1932, M. Caneda.

Description

Holotype, male. Size, $5.5\ \text{mm} \times 2.2\ \text{mm}$; elongate, ovoid, transversely subconvex above and below; both surfaces reddish cupreous, head with a golden reflection; head and underside moderately shallowly punctate; pronotum imbricate; elytra rugose discally, imbricate laterally; surface with very sparse cover of short, white, adpressed setae; elytra with setae slightly more stout and more dense and with subsquamiform setae in one fascia and one patch on each elytron as in fig. 60.

Head: slightly produced between eyes on either side of longitudinal depression of frons; eyes large, inner margins feebly diverging dorsally; ventral arch of eye bordered by moderately deep groove; frontoclypeus with vague transversely sinuate supraantennal groove; disc constricted between large antennal cavities; distal margin with trapezoidal emargination, oblique laterally, truncate medially; gena grooved beneath eye for antenna in repose, projecting lobe acute. Antennae: antennomere 1 gibbose; 2 slightly shorter than 1, narrower; 3 shorter than 2, slightly wider distally; 4 9 subrectangularly serrate, length subequal to width; 10 and 11 missing.

Pronotum: nearly $2\times$ as wide as long, widest in posterior half; anterior margin biarcuate on either side on medial convexity; posterior margin bisinuate on either side of median truncate lobe, a pre-



Figs. 56-59, *Philocoroebus* spp., dorsal and lateral habitus. – 56, 57, *P. pseudocisseis* sp. n.; 58, 59, *P. elongatus* sp. n. (scale lines = 1 mm).

marginal carina extends between two arcuations medially; posterolateral angles obtuse, rounded; lateral margins only visible at base when viewed directly from above, carinate, subparallel from posterior margin to beyond midpoint, then arcuate to anterior margin; disc flattened, slightly depressed in posterolateral thirds; premarginal carinae nearly entire, not reaching either anterior or posterior margin. Scutellum: cordiform.

Elytra: slightly wider than pronotum, widest at margin opposite humeri; lateral margins subparallel from base to about apical third, then gradually attenuate to separately rounded apices; margins appear serrulate due to lateral imbrications; epi-

pleuron very short, only feebly separated from disc; disc feebly transversely convex; each elytron depressed at base between humerus and scutellum and declivous past humerus posterolaterally; distal portion of pygidium slightly visible beyond elytral apices.

Underside: prosternum with bilobed mentoniere, process with sides subparallel between procoxae, apex broadly rounded; metacoxal plate short, margins subparallel, posterior margin sinuate, feebly dilated; abdominal sternites with sutures between 2, 3, 4 and 5 transverse medially, arcuate laterally; length of 1 less than $2 + 3$; $1 + 2$ slightly longer than $3 + 4 + 5$; 2-5 with premarginal groove; 5 with marginal band strongly explanate, a moderately dense fringe of long white recumbent setae on disc before premarginal groove; marginal attenuate laterally, then arcuate to slight median emargination. Leg: femora feebly swollen, sides subparallel; protibia feebly arcuate, slightly flattened; metatibia nearly straight, subcylindrical; protarsi with tarsomeres 1-4 each progressively shorter, with ventral pulvilli progressively longer, more expanded; metatarsi with antennomere 1 elongate slightly longer than $2 + 3$; 5 narrow, with stout simple claws.

Genitalia: as in fig. 62, mounted on point with specimen. The holotype is damaged with the following parts missing: left antennae, last two antennomeres; right antennae, last three antennomeres; left fore leg and middle leg missing most of tibiae and complete tarsi; right middle leg missing entire tibia and tarsus; left hind leg missing entire tarsus.

Remarks. – The only revision of *Cisseis* was by Carter (1923) and was only for the Australian species. To even discuss this new Philippine species in context of the Australian species and Carter's revision without considering the remaining complement of *Cisseis* seems rather moot and such discussion would obviously be rather misapplied. However, for comparative purposes, the following discussion may aid the reader in his understanding of this new Philippine species and its, at least superficial, relationship to the Australian congeners. *C. aquilonia* belongs to the group Carter categorized as 'Sect. II, Group B', those with the elytra vaguely impressed with white pubescence, more or less marbled, but not in circular spots. The key Carter provides for this group is partly based on colour without a clear outcome for *aquilonia*. A reasonable comparative match is with *C. roseocuprea* Hope, which compares well in size and coloration, but differs by not having the flattened white elytral setae, but has the lateral pronotal carinae visible from above and the general dorsal sculpture is both denser and the elytra more rugose. The few

non-Australian *Cisseis* spp. listed by Obenberger (1935) will need to be validated as to their correct generic placement in contrast to *Anocisseis* Bellamy (1990), now known from the Philippines and Borneo.

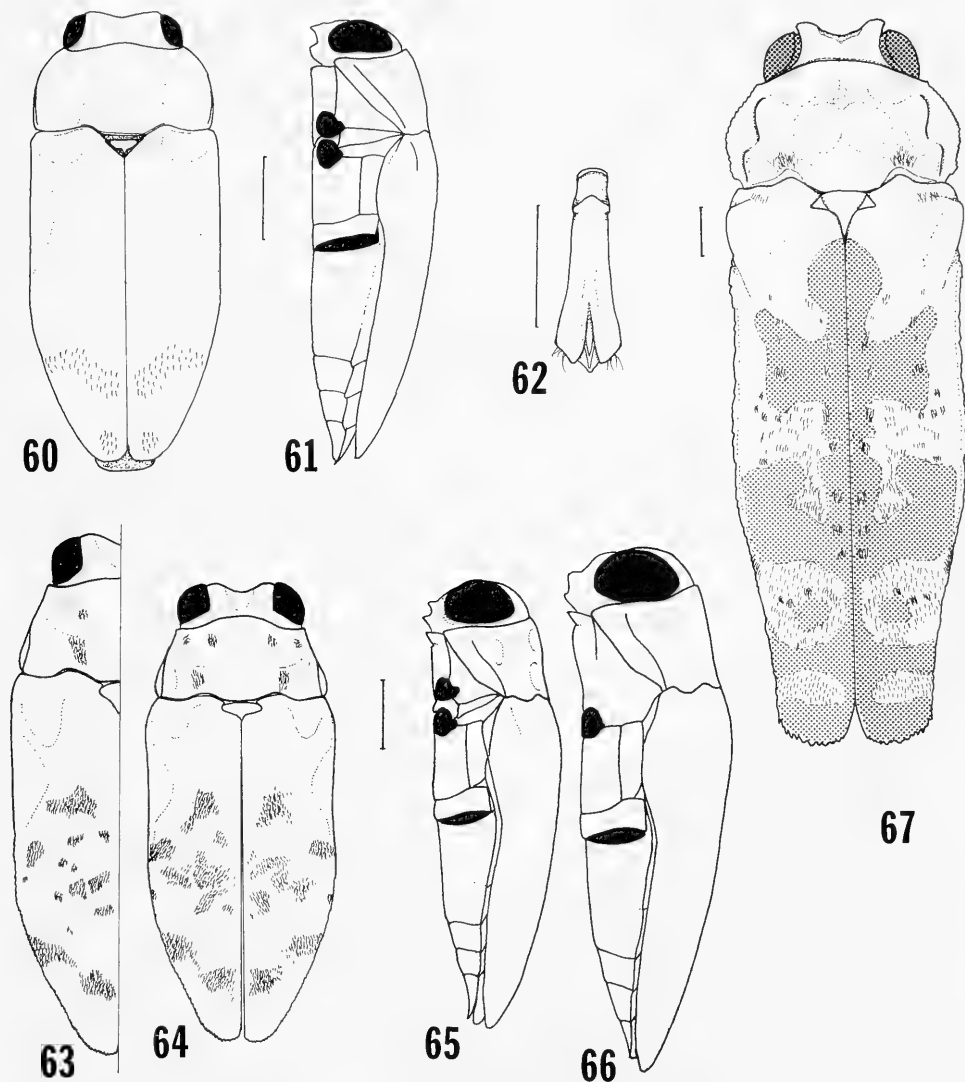
Genus *Anocisseis* Bellamy

Anocisseis Bellamy, 1990: 693. – Type-species: *Anocisseis samarensis* Bellamy [from original designation].

Remarks. – This genus and the type-species were fully described in the first part of this series (Bellamy 1990). I have included them here only in context to the generic key and refer the reader to the previous paper for more detail.

Genus *Hypocisseis* Thomson

Hypocisseis Thomson, 1879: 49. – Kerremans 1893: 118; 1903: 256; Obenberger 1935: 860; Bellamy 1985: 425;



Figs. 60-67. *Cisseis*, *Hypocisseis* and *Vanroonia* spp. – 60-62, *C. aquilonia* sp. n.; 60, dorsal habitus; 61, left lateral aspect; 62, male genitalia, dorsal aspect; 63, 66, *H. auriceps*; 63, left dorsal habitus; 66, left lateral aspect; 64, 65, *H. philippinensis* sp. n.; 64, dorsal habitus; 66, left lateral aspect; 67, *V. luzonica* sp. n., dorsal habitus (scale lines = 1 mm).

1988: 417. – Type-species: *Hypocisseis laticornis* Thomson [from original monotypy].
Cisseoides Kerremans, 1893: 118. – Kerremans 1903: 254; Obenberger 1935: 857; Bellamy 1985: 425. – Type-species: *Cisseoides murina* Kerremans [from original monotypy].

Remarks. – These taxa were discussed recently by Bellamy (1988). *Hypocisseis* would benefit from a thorough revision and this new species is described to encourage such a project.

***Hypocisseis philippinensis* sp. n.**
 (figs. 64, 65)

Type material. – Holotype, female (BPBM 14608): P. I., Mindanao, Zamboange del Sur, Lemesahan, 600m, 7.IX.1958 / light trap, H. E. Milliron.

Description

Holotype, female. Size, 6.6 mm × 2.7 mm; elongate, ovoid, transversely subconvex above and below; nitid black with cupreous reflections on imbrications of vertex and pronotum, elytra with aeneous reflection; head with most of frontal area bright roseocupreous; head, pronotum and ventral surface imbricate, elytra imbricate rugose; surface generally sparsely setose with setae short, white, recumbent, those on elytra subsquamiform.

Head: large eyes slightly produced on either side of frontal depression; inner margins of eyes subparallel; frontoclypeus with a transverse groove dorsal; disc constricted between large antennal cavities; distal margin with half-trapezoidal emargination; gena with area along ventral margin of eye excavated, ventral to this transversely grooved for antennae in repose and projecting lobe acute; antennae with antennomere 2 shorter, more slender than 1; 3 shorter than 2; 4-6 triangular serrate; 7-10 rectangularly serrate; 11 oblong, recurved distally.

Pronotum: width 2X length, widest near base; anterior margin broadly arcuate; posterior margin bisinuate on either side of median prescutellar lobe; basolateral angles obtuse; lateral margins broadly arcuate in posterior half then more straight and converging toward anterior margin; single carina on either side extending from posterior margin to about anterior third; disc uneven, with slight depressions in pairs which are filled in by concentrations of setae as in fig. 64; scutellum broadly cordiform, posterior angle acute.

Elytra: slightly wider at humeri than pronotum; humeri moderately elevated; lateral margins roundly acute from base to opposite humeri, the subparallel to about apical third before gradually narrowing to separately rounded apices; margins carinate serrate from near midpoint; epipleuron a

small, elongate triangle; disc with slight basal depression on either side; setal pattern as in fig. 64; pygidium not visible past apices.

Underside: prosternum with bilobed mentonniere; process with sides subparallel between procoxae, apex triangularly attenuate; metacoxal plate short, moderately dilated; abdominal sternites 1 + 2 slightly longer than 3 + 4 + 5; sutures between 2, 3, 4 & 5 evenly transverse; sternite 5 with pre-marginal groove concentric to margin, with a sparse row of elongate testaceous setae projecting toward posterior, apex slightly emarginate.

Legs: femora feebly fusiform, ventral surface slightly excavated for tibiae in repose; protibiae slightly arcuate at base, feebly flattened, unarmed at apex; meso- and metatibiae straight, subcylindrical; tarsomeres 1-4 each progressively slightly longer, with ventral pulvilli more developed distally; 5 elongate, narrow, claws bifid with inner teeth shorter. This specimen is missing the entire left hind leg.

Remarks. – The species listed under *Cisseoides* by Obenberger (1935) are either from Australia or New Guinea. *H. philippinensis* represents the first species known from north of the Equator, an obvious significant range extension for the genus. I have illustrated the new species in comparison to *H. auriceps* (Deyrolle) (figs. 63, 66) from New Guinea. These two species differ in their proportions, coloration, vestiture, shape and configuration of the prelaternal pronotal carinae.

Genus *Vanroonia* Obenberger

Vanroonia Obenberger, 1923: 29. – Obenberger 1935: 814; 1958: 503; Bellamy 1985: 425; 1988: 416. – Type-species: *Vanroonia coraeoides* Obenberger [from original monotypy].

Remarks. – This genus and its identity in comparison to *Amorphosoma* Laporte was discussed by Bellamy (1988, 1990). The relictual nature of the species of *Vanroonia* is indicated by the spread of their distribution (i.e. Africa, India, S.E. Asia, Philippines). An eventual revision of *Vanroonia* would be helpful as an adjunct to that of Obenberger (1958). Two species are now known from the Philippines as discussed below.

***Vanroonia marmorea* (Deyrolle)**

Amorphosoma marmoreum Deyrolle, 1864: 127. – Obenberger 1935: 793; Fisher 1921: 408; 1926: 241. *Vanroonia marmorea*; Bellamy 1990: 692.

Remarks. – This species, as discussed by Fisher

(1921, 1926) and Bellamy (1990), is well defined and will be distinguished from its new congener below.

Vanroonia luzonica sp. n.
(fig. 67)

Type material. – Holotype, female (USNM): Quezon Park, Tayabas, P. I., Alt. 1000 ft., VII-1-[19]32 / F. C. Hadden Collector.

Description

Holotype, female. Size, length 15.0 mm, width (of pronotum) 4.6 mm; elongate, subcylindrical, flattened below; shining black, with some areas of venter, especially epipleuron, reflecting blue purple; head, pronotum and underside generally imbricate, elytra rugose; surface generally sparsely covered by short recumbent white setae from imbricate punctures, setae longer and/or more dense in some areas of pronotum and elytra as shown in fig. 67; elytra with short white setae in patterns and stout, semi-erect dark brown setae interspersed on disc (fig. 67, stippled area).

Head with frontovertex depressed medially, produced into lateral lobes which project beyond ocular margin; eyes large, subreniform, inner margins feebly sinuate, diverging dorsally; ocular groove extends from slightly beyond dorsal apex along inner margin to before ventral apex, quite wide dorsally; supraantennal groove transverse, bi-arcuate; frontoclypeus compressed between antennal cavities, distal margin excavated, straight medially, arcuately laterally; gena with large acute projecting tooth ventral to each eye. Antenna with antennomere 1 stout, geniculate basally; 2 shorter, narrower than 1; 3 shorter than 2; 4-10 serrate, 4 with width subequal to length, 5-10 each with width to length ratio increasing; 11 oblong.

Pronotum nearly 2X wider than long, widest at middle; anterior margin arcuate; posterior margin strongly bisinuate on either side of median lobe; basolateral angles obtuse; lateral margins broadly arcuate, crenulate, explanate; disc uneven, subtuberculate, with biarcuate prelateral carina on either side. Scutellum large, wider than long, anterior margin straight, with angulate lateral lobes, distal lobe acuminate; disc finely rugose.

Elytral subequal in width to pronotum, widest at humeri; humeral lobes feebly projecting; one moderately deep depression at base between humerus and scutellum on either side; lateral margins carinate, widely serrate, subparallel from humeri to apical third, then narrowing gradually to broad, separately rounded, dentate apices; disc flattened medially, convexly rounded laterally; epipleuron

widest just beyond base, subparallel to opposite metacoxa, then gradually narrowing to apicolateral elytral angle.

Underside. Prosternum shortened, mentonniere angularly bilobed, process slightly compressed between procoxae, attenuately rounded apically; metacoxae short, dilated apically; abdominal sternites 1+2 longer than 3+4+5; 5 with preapical groove around entire length, apex straight.

Legs. Femora narrowly fusiform; tibiae somewhat flattened, with a quadrate cross-section, with two short stout spines on inner margin distally; protibiae arcuate basally; tarsi short, tarsomeres 1-4 subequal, each progressively shorter and with progressively longer ventral pulvillus; 5 narrow, elongate, equal in length to 1-4 together, claws simple.

Genitalia. Ovipositor mounted on card beneath specimen; of 'coroebine type'.

Remarks. – The name is chosen for Luzon, the large northern island of the Philippine archipelago and location of the type locality. This new species can be distinguished from *V. marmorea* by its larger size, black coloration and elytral vestiture. *V. marmorea* usually has the two projecting lobes on the frontovertex clothed with dense erect stout testaceous setae. In addition, the head, pronotum and basal two-thirds of the elytra are a dull aeneous colour and most of the thoracic sternites are densely covered with adpressed white setae.

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REVISION OF THE GENUS *CHAMPAKA* (HOMOPTERA, CICADIDAE) FROM BORNEO AND SULAWESI

Duffels, J. P., 1991. Revision of the genus *Champaka* (Homoptera, Cicadidae) from Borneo and Sulawesi. – Tijdschrift voor Entomologie 134: 177-182, figs. 1-7. [ISSN 0040-7496]. Published 18 December 1991.

The genus *Champaka* and its species are redescribed. The genus includes *C. celebensis* (= *C. maculipennis* syn. n.) from NW Sulawesi and *C. viridimaculata* (= *C. harveyi* syn. n.), a widespread species in Borneo. Lectotypes are designated. The relationships of *Champaka* are discussed.

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During our ongoing studies of the cicadas of Sulawesi, we have noted that the cicada-fauna of this island is highly endemic and a mixture of taxa with Oriental and Australian relationships (Duffels 1990). The cicada genus *Champaka* Distant, 1905, revised in the present paper, has Oriental affinities. The distribution of the genus reflects a biogeographic coherence between Sulawesi and Borneo.

The genus *Champaka* was erected by Distant (1905) for *Pomponia viridimaculata* Distant, 1889, from North Borneo, which is thus the type-species by monotypy. Later, the same author added two other species to the genus, viz., *Champaka harveyi* Distant, 1912 from Borneo and *Champaka celebensis* Distant, 1913 from Celebes [= Sulawesi]. Some years later Haupt (1917) described *Champaka maculipennis* from Celebes. The present study reveals the synonymy of the types from Borneo, as well as those from Sulawesi.

DEPOSITORYES

Abbreviations for depositories of material used in this paper: Natural History Museum (formerly: British Museum (Natural History)), London, United Kingdom (BMNH); California Academy of Sciences, Department of Entomology, San Francisco, USA (CAS); Deutsches Entomologisches Institut, Eberswalde, Germany (DEI); National Museum of Natural History (formerly: Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH); private collection Professor Dr. H. J. Müller, Jena, Germany, containing H. Haupt's

Homoptera collection (Coll. Müller) and Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam, The Netherlands (ZMA).

TAXONOMY

The references to the genus and the species are a selection of the most relevant literature; further references can be obtained from the catalogues by Metcalf (1962, 1963) and Duffels & Van der Laan (1985).

Champaka Distant

Champaka Distant, 1905: 60, 70. – Distant 1906: 49, 71; Distant 1912: 39, 56; Moulton 1923: 82, 116, 166. – Type-species by monotypy: *Champaka viridimaculata* (Distant, 1889).

Diagnosis. – Postclypeus globular. Head considerably broader than mesonotum. Head about as long as wide between eyes. Male abdomen considerably longer than head and thorax together. Lateral margins of pronotum amplified and distinctly toothed at midlength. Male operculum triangular, short, reaching just beyond anterior margin of abdominal segment 3 or to half-length this segment. Greatest width of tegmen less than a third of its length.

Characterization of the genus *Champaka* by synapomorphies must await phylogenetic analysis of the characters of the species of *Champaka* and related genera. The combination of the elongate body-shape and the short opercula of the male



Figs. 1-2. *Chompaka* ssp., habitus, males. – 1, *C. viridimaculata*, Brunei, Badas; 2, *C. celebensis*, Sulawesi, Palu, 1985.

traditionally separates *Chompaka* from other genera. The *Chompaka* species resemble *Platylomia spinosa* (Fabricius, 1787) and related species in the relatively long abdomen, the broad head and the similar body colour and marking, in spite of the long male operculum of these *Platylomia* species. The structure of the male genitalia is like those found in *Platylomia* and other related genera.

Key to the species of *Chompaka*

1. Tegmen with infuscations at bases of 2nd, 3rd, 5th and 7th apical areas and along posterior longitudinal vein of 7th apical area. Male operculum as in fig. 5 and reaching to half length abdominal segment 3 or to almost posterior margin of this segment. Male genitalia as in fig. 3 (Sulawesi) *C. celebensis* Distant
- Tegmen with infuscations at bases of 2nd and 3rd apical areas. Male operculum as in fig. 6 and reaching just beyond posterior margin of abdominal segment 2. Male genitalia as in fig. 4 (Borneo) *C. viridimaculata* (Distant)

Chompaka celebensis Distant (figs. 2, 3, 5, 7)

Chompaka celebensis Distant, 1913: 80. – Lectotype ♂

[here designated]: 'N.W.Celebes / (de Giacomi)' [handwritten], 'Chompaka / celebensis / Dist. type' [Distant's writing], 'Type' [print; red margined label], 'Distant coll. / 1911-383' [print] (BMNH) [examined].

Chompaka maculipennis Haupt, 1917: 305. – Lectotype ♂ [here designated]: 'Paloe / N. W. Celebes', 'Chompaka ♂ / maculipennis Hpt' (Collection Müller) (syn. n.) [examined].

Other material examined: 1 ♂ paralectotype *Chompaka celebensis*, N.W. Celebes, de Giacomi, Distant coll. 1911-383 (BMNH); 2 ♂, Paloe, N. W. Celebes, A. Heyne, *Chompaka bellicosa* Mel. (manuscript name) (DEI). These two specimens may belong to the type series of *Chompaka maculipennis*, which consists of four males from Palu collected by A. Heyne, but the absence of Haupt's identification labels and the presence of the label with Melichar's manuscript name refrain me from labelling these specimens paralectotype; 1 ♂, Sulawesi, Palu, 27.xi.1985, at light, J. van Tol (RMNH).

Description of the male

Ground colour of body brown; ground colour of dorsal surface of head, pronotum and lateral parts of mesonotum olive-green in the specimen collected in 1985. Head and thorax silvery pilose with exception of mediodorsal part of pronotum, dorsal surface of pronotal collar and greater part of me-

sonotum disk; abdomen dorsally with scattered silvery pilosity in a median and two lateral bands. Underside of body somewhat lighter brown.

Head: Postclypeus for the greater part dark castaneous with medial, oval, greenish spot at anterior margin and light brown lateral parts. A round black spot enclosing the ocelli; three pairs of very small spots are situated laterally of ocelli. Rostrum with dark brown apex passing hind coxae.

Thorax: Pronotum with one broad, dark castaneous, central fascia which widens to the anterior and to the posterior, a pair of juxtaposed or fused, small, black spots in the central fascia just in front of pronotal collar, a pair of fairly large, half-moon shaped, black-brown spots between the two pairs of oblique fissures and two pairs of short, narrow, black-brown lines just above and below proximal ends of posterior oblique fissures. The narrow, black-brown coloration of posterior oblique fissures broadens distally and continues along lateral part of ambient fissure as a fascia of variable width. Pronotal collar laterally with dark suffusion. Mesonotum with vague median fascia, a pair of narrow, black-brown, slightly converging paramedian fasciae reaching to half the mesonotum length, a pair of small, round, black-brown spots in front of cruciform elevation and a pair of very broad lateral fasciae on posterior half or two-thirds of mesonotum. Cruciform elevation lighter than mesonotum disk; anterior arms of cruciform elevation with distinct dark mark.

Tegmina and wings: Hyaline. Venation ochreous to light brown variegated with black-brown; basal cell and extreme basal venation of tegmen of specimen collected in 1985 with light greenish tinge. Tegmina with infuscations around transverse veins at bases of 2nd, 3rd, 5th and 7th apical areas; infuscation at base of 7th apical area extending along posterior vein of this area. Lectotype of *celebensis* with very small, marginal spots at apices of longitudinal veins of tegmina; most of these spots are missing in the other specimens.

Legs: Fore femora black-brown with yellowish basal or middle part; middle and hind femora castaneous brown, middle femora with black-brown anterior line. Tibiae of all legs and tarsi of fore and middle legs castaneous brown (tarsi of hind legs missing).

Operculum (fig. 5): Triangular, light brown, with almost straight lateral and medial margins and a subacutely rounded apex, reaching to half-length abdominal segment 3 or to almost posterior margin of this segment.

Abdomen: Castaneous brown dorsally and light brown ventrally, very long, about 1.4 times as long as head and thorax together. Timbal covering with weakly convex anterior margin and weakly con-

cave lateral margin

Genitalia (fig. 3). Pygofer one and a half times as long as wide; widest at half-length. Both, lateral margins of apical half of pygofer and sides of basal cup of pygofer pronounced. Uncus lobes broad, lateral margins weakly concave, apical margin weakly convex to attenuate laterodistal corner.

Measurements in mm (6 ♂). Body length 49.0-61.0 (52.9 ± 3.8); head width 13.8-15.5 (14.5 ± 0.7); pronotum width 14.7-16.4 (15.3 ± 0.6); tegmen length 55.7-62.5 (60.5 ± 2.3).

Distribution (fig. 7)

This species was collected in Palu and in an unknown locality in NW Sulawesi. The specimen from Palu in the RMNH was collected from a window-pane of a restaurant in town in 1985. In spite of rather intensive collecting near Palu and in other areas of Sulawesi in recent years, no more specimens of this species became available.

Champaka viridimaculata (Distant)

(figs. 1, 4, 6, 7)

Pomponia viridimaculata Distant, 1889: 421. – Lectotype ♂ [here designated] 'Kina Balu / (Whitehead)' [handwritten], 'viridi- / maculata / Dist' [handwritten], 'Type' [print; red margined round label], 'Distant coll. / 1911-383' [print] (BMNH) [examined].

Pomponia viridimaculata; Distant 1891: 73, Pl.X, figs. 9, 9a-b; Distant 1892: xii; Breddin 1900: 180.

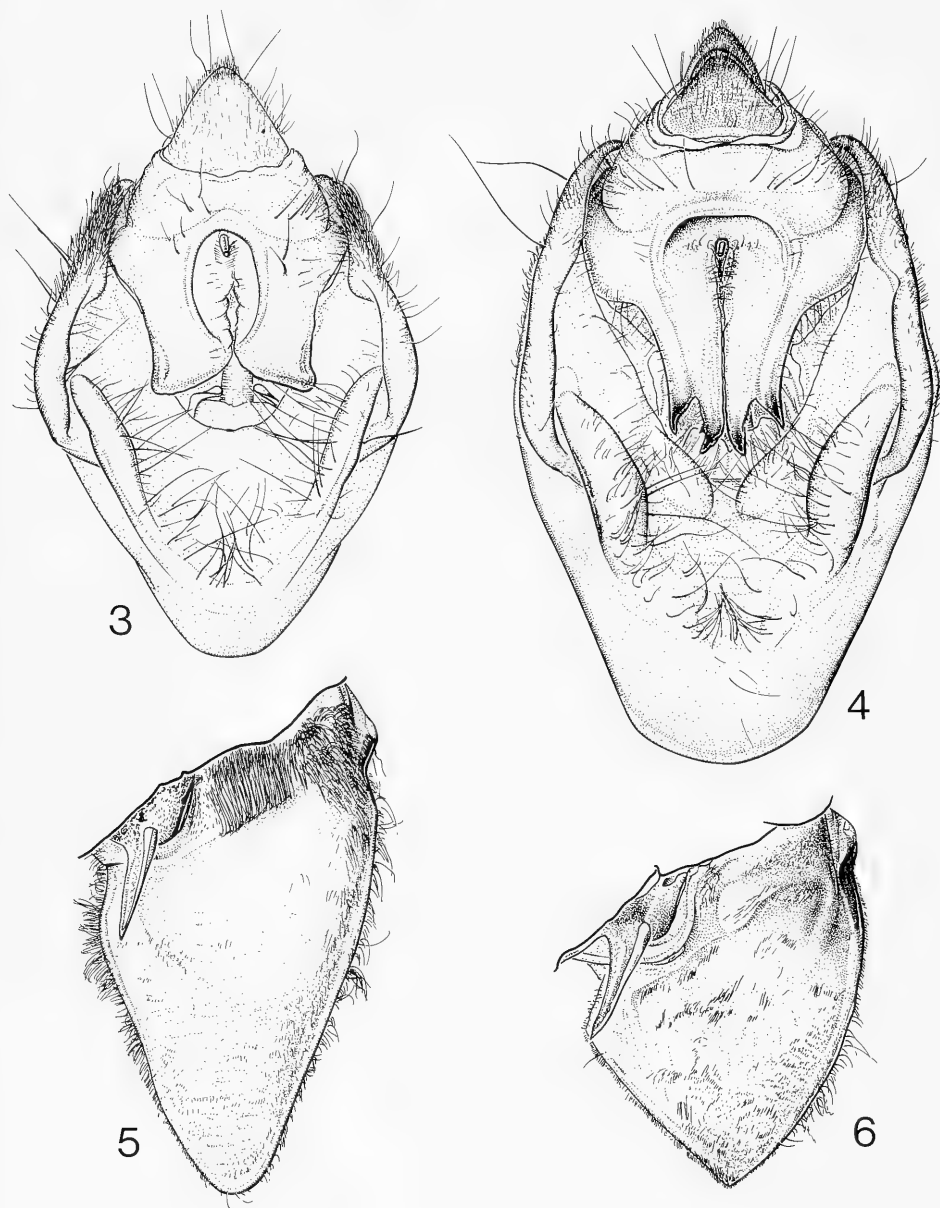
Champaka viridimaculata; Distant 1905: 66, 70; Distant 1906: 71; Distant 1912: 57, Pl. 6, figs. 49a-c; Distant 1913: 80; Haupt 1917: 306; Moulton 1923: 116, 168.

Champaka harveyi Distant, 1912: 57. – Holotype ♂: 'Dutch Borneo / Balakpappan / Henry Harvey / 1912-324' [handwritten], 'Champaka / harveyi / Dist. type' [Distant's writing], 'Type' [print; red margined round label] (BMNH) [examined] (syn. n.).

Champaka harveyi; Moulton 1923: 116, 168.

Champaka viridimaculata harveyi; Haupt 1917: 306.

Other material examined. – 1 ♂ paralectotype *Pomponia viridimaculata*, Kina Balu, Whitehead, Distant coll. 1911-383 (BMNH). Indonesia, Kalimantan: 2 ♂, Pontianak, Borneo Exp., Max Weber (RMNH); 1 ♂, Sambas, Dr. J. Bosschoo, acq. 1891 (RMNH); 1 ♂, Sanga Sanga, H. D. Jansen, 1907-203 (BMNH). – Malaysia, Sabah: 2 ♂, Mt. Kinabalu, Tenom Keningau, 4-8.iii.1964, J. Smart, Royal Soc. Exped., B. M. 1964-250 (BMNH); 1 ♂, Labuan, 99-279, *viridimaculata*, Dist. (BMNH); 5 ♂, Poring, 9 mi. N. of Ranau, 1600', 26-29.iv.1970, T. W. & M. C. Davies (CAS); 1 ♂, Tawau, 10.iv.1970, G. Mendenhall, coll. T. W. Davies (CAS); 3 ♀, Tawau, Brumas Camp, xi.1974, C. Pruett, B. M. 1975-590 (BMNH); 8 ♀, Sandakan Dist., Rumidi, R. Labuk, 16-30.ix.1973, C. Pruett, B. M. 1975-590 (BMNH). – Malaysia, Sarawak: 1 ♂, Bidi, 1907-1908, C. J. Brooks (BMNH); 2 ♂, Kedurong, Moulton, Distant coll. 1911-383 (BMNH); 4 ♂, Kedurong, iii.1911, J. C. Moulton, 1911-141 (BMNH). – Brunei: 5 ♂, Brunei,



Figs. 3-6. *Champaka* ssp. – 3, Male pygofer in ventral view, *C. celebensis*, Sulawesi, Palu, 1985; 4, Idem, *C. viridimaculata*, Brunei, Badas; 5, Male operculum in ventrolateral view, *C. celebensis*, Sulawesi, Palu, 1985; 6, Idem, *C. viridimaculata*, Brunei, Badas.

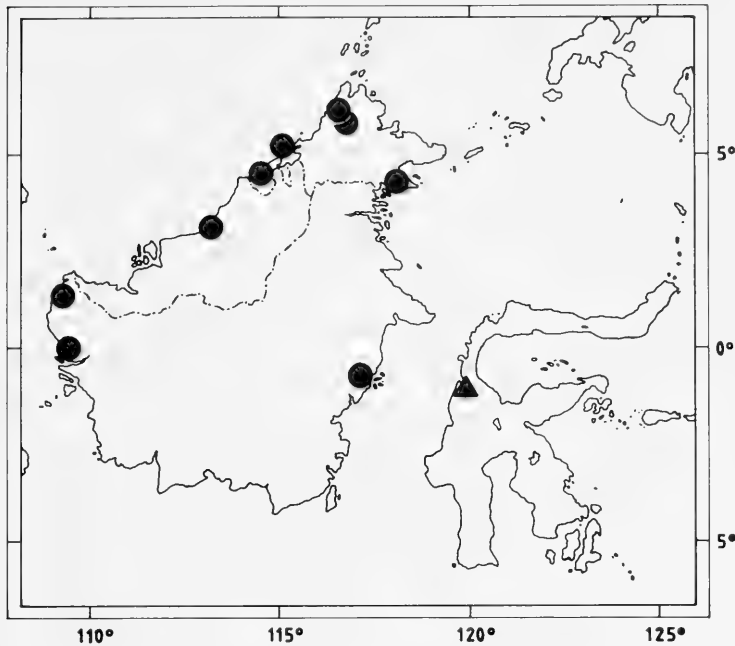


Fig. 7. Distribution of *Champaka viridimaculata* (black dots) and *Champaka celebensis* (triangle).

Waterstradt (BMNH); 2 ♂, Brunei, booreiland voor de kust (drilling platform off the coast), acq. 1969, C. Krannenburg (ZMA); 9 ♂, Badas, *Agathis* / swamp forest / secondary vegetation, 27.ii.1982, 50-100', G. S. Robinson, 1982-156 (BMNH); 5 ♂, Rampayoh R. (north), LP 195, lowland forest, 1-3.iii.1982, 100', G. S. Robinson, B M 1982-156 (BMNH); 1 ♂, S. Selanjak, 4464.1432, mangrove, 0 m, 8-9.iii.1984, Maj. T. P. G. Helps, B. M. 1984-296 (BMNH).

Synonymy

C. harveyi was separated from *C. viridimaculata* by the immaculate tegmina, the greyish-white basal membranes of tegmina and wings and the more pointed male operculum. Study of the holotype of *C. harveyi* led to the conclusion that this specimen is an immature *C. viridimaculata*. The holotype of *harveyi* has very faint, but still recognizable spots on the tegmina. White basal membranes in the tegmina and wings are also found in specimens of *C. viridimaculata*. The opercula of *harveyi* seem to be more pointed but this is an artefact due to deformation of the soft body.

Description

Body brown to dark brown or black-brown with exception of some parts of mesonotum and pronotum collar, which are light brown or lightly greenish tinged; abdomen of both sexes often castaneous. Pilosity on body as in *C. celebensis* but

underside of head, with exception of postclypeus, more thickly covered with long silvery hairs.

Head: Postclypeus more globular than in *C. celebensis*; colour dark castaneous with medial, oval, light ochreous to light brownish spot. A black spot encloses the ocelli and a pair of large dark spots is situated between ocelli and eyes. Rostrum dark brown to apex and just reaching posterior margin of hind coxae.

Thorax: Pronotum with an, often indistinct, marking consisting of a pair of central fasciae, a pair of spots between the two pairs of oblique fissures and a dark coloration in these oblique fissures. Mesonotum shiny and often darker brown than pronotum but without discernible marking.

Tegmina and wings: Hyaline. Colour of venation of tegmen as in *C. celebensis*. Transverse veins of 2nd and 3rd apical areas of tegmen infuscated. A distinct brown spot is found at apex of anterior longitudinal veins of 2nd apical area, while some specimens have two or three more, very small, marginal spots. Basal membranes of tegmina and wings vividly green. Legs as in *C. celebensis*.

Male. Operculum (fig. 6): Triangular, dark brown, with an almost straight medial margin, a weakly convex lateral margin, and an about rectangular apex reaching just beyond posterior margin of abdominal segment 2.

Abdomen: Castaneous brown to black brown dorsally and somewhat lighter ventrally, very long, 1.3-1.5 times as long as head and thorax together.

Timbal covering distinctly broader than in *C. celebensis*, leaving a smaller part of interior timbal cavity exposed; lateral margin of timbal covering straight or very slightly convex.

Genitalia (fig. 4): Pygofer somewhat less than twice as long as wide, widest at half-length. Lateral margins of apical half of pygofer and curved ridges forming sides of basal pygofer cup strongly pronounced. Uncus with two lobes narrowing to apices. Apex of uncus lobe bidentate, medial teeth of both lobes juxtaposed and slightly recurved, lateral tooth triangular.

Female. Operculum: Semicircular shaped and with slightly convex surface covered with scattered pilosity. Operculum reaching just beyond posterior margin of abdominal segment 2.

Abdomen: Castaneous brown dorsally and somewhat lighter ventrally. Dorsal surface scattered silvery pilose. Abdomen 0.9-1.2 times as long as head and thorax together.

Measurements in mm (10 ♂, 8 ♀). Body length ♂ 51.5-56.0 (53.8 ± 1.5), ♀ 36.6-49.2 (42.5 ± 4.8); head width ♂ 15.2-15.8 (15.5 ± 0.3), ♀ 12.7-15.8 (14.8 ± 1.1); pronotum width ♂ 15.5-17.5 (16.2 ± 0.6), ♀ 12.3-17.1 (15.0 ± 1.7); tegmen length ♂ 51.0-66.2 (63.1 ± 1.7), ♀ 51.7-64.7 (57.6 ± 4.6).

Distribution (fig. 7)

This species is an endemic of Borneo and recorded from lowland localities only.

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NEW SPECIES OF THE GENUS *MEGACOELUM* FIEBER FROM CHINA (MIRIDAE, HETEROPTERA)

Li, X. Z. & L. Y. Zheng, 1991. New species of the genus *Megacoelum* Fieber from China (Miridae, Heteroptera). – Tijdschrift voor Entomologie 134: 183-192, figs. 1-45. [ISSN 0040-7496]. Published 18 December 1991.

Seven new species of the genus *Megacoelum* Fieber from China are described: *M. pronotalis*, *M. chinensis*, *M. rubripedum*, *M. pseudopronotalis*, *M. zoui*, *M. tenuicorne* and *M. yunnanum*. *M. fuscescens* Hsiao, 1963 is redescribed.

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Key words. – China; *Megacoelum*; Miridae; new species.

The genus *Megacoelum* Fieber was established in 1858. Since then more than 60 species have been described, most of them distributed in the Old World tropics and subtropics (Distant 1904, 1910, Oshanin 1910, Poppius 1914, Carvalho 1959, Linnavuori 1963-1975, Wagner 1970/1971, Kershner 1972). Up to now, only three species were recorded from China. Two of them were described from Taiwan (*M. minutum* and *M. clypeale*) by Poppius (1915), and the third (*M. fuscescens* Hsiao, 1963) was described from Yunnan (Hsiao & Meng 1963). Seven new species, found in China, are described in this paper, and *M. fuscescens* Hsiao is redescribed.

Megacoelum minutum and *M. clypeale* are only included in the key. A redescription of these species could not be provided since the types were not accessible to us.

In the descriptions, 'body length' = the distance from head apex to hemelytral apex, 'body width' = the maximum width across both hemelytra at repose, 'head length' = the length in front view, and 'pronotum length' = the length including collar. Measurements are given in millimeters. In the figures of the vesicae, the secondary gonopore is dorsally directed.

The material cited in this paper was all collected in China. The types of the new species are deposited at the Biology Department of the Nankai University except where mentioned otherwise. TJNM means Tianjin Natural Museum, China.

Checklist of Chinese species of *Megacoelum*

Megacoelum pronotalis Li et Zheng sp. n.

(Zhejiang, Jiangxi, Shanxi)

Megacoelum chinensis Li et Zheng sp. n.

(Zhejiang, Fujian)

Megacoelum rubripedum Li et Zheng sp. n.

(Fujian)

Megacoelum pseudopronotalis Li et Zheng sp. n.

(Fujian)

Megacoelum zoui Li et Zheng sp. n. (Yunnan)

Megacoelum tenuicorne Li et Zheng sp. n.

(Guangdong, Guangxi, Sichuan)

Megacoelum yunnanum Li et Zheng sp. n.

(Yunnan)

Megacoelum fuscescens Hsiao, 1963. (Guangdong,

Guangxi, Hainan, Yunnan)

Megacoelum clypeale Poppius, 1915. (Taiwan)

Megacoelum minutum Poppius, 1915. (Taiwan)

Key to the Chinese species of *Megacoelum*

1. Cuneus yellow with black apex. Outer basal angle of membrane with a whitish spot. Body small, length 5mm *minutum* Poppius
- Cuneus at least basal 2/3 black, membrane unicolorously dark smoky 2
2. Black, with calli and areas before and behind reddish brown. Pronotal basal margin narrowly yellow, embolium and outer cuneus reddish, apical third of cuneus yellowish brown *yunnanum* sp. n.
- Calli concolorous with pronotum. Hemelytra differently coloured 3
3. Pronotum medially with black markings ... 4



Figs. 1-5. *Megacoelum fuscescens* Hsiao. - 1, vesica in dorsal view; 2, spicule; 3, 4, left clasper, 5, right clasper.

- Pronotum without black markings 6
- 4. Pronotum with a triangular black spot at anterior margin, a round median black spot at hind margin of calli, and a long black spot at hind margin. Rostrum only reaching to apex of mesocoxae *clypeale* Poppius
- Pronotum with only one percurring median black marking 5
- 5. Pronotal median black marking broad and well-defined. Pubescence sparse and long *pronotalis* sp. n.
- Pronotal median black marking vague and slender: Pubescence very dense and short *zoui* sp. n.
- 6. Pubescence dense and short. Pygofer without a knob before left clasper ... *rubripedum* sp. n.
- Pubescence sparse and long. Pygofer with a knob before left clasper 7
- 7. Pronotal lateral margin and basal portion darkened, extreme basal margin yellowish brown *fuscescens* Hsiao
- Pronotum unicolorous 8
- 8. Frons with reddish transverse stripes. Clypeus somewhat prominent. Antennae slender *tenuicorne* sp. n.
- Frons without light-colored stripes 9
- 9. Knob on pygofer before left clasper very short. Body comparatively short and broad. Length 6.88-8.74 *chinensis* sp. n.
- Knob on pygofer before left clasper large and sharp. Body slender, length 8.37-8.56 *pseudopronotalis* sp. n.

DESCRIPTIONS

1. *Megacoelum pronotalis* sp. n. (figs. 6-10)

Type material. - Holotype male: Mt. Tianmu (30° 24'N, 119° 30'E), Zhejiang Prov., 15.viii.1965, L. C. Wang leg. - Paratypes: 5 males, 3 females, with same data as holotype; 12 males, 19 females (TJNM), same data as holotype, S. L. Liu leg.; 6 males, 1 female, Mt. Lushan (29° 24'N, 115° 54'E), Jiangxi Prov., 22/24.vii.1957, S. H. Ying leg.; 1 male, 5 females (TJNM), Ku-ling (29° 24'N, 115° 54'E), Jiangxi Prov., 10. vii/7.viii.1935, O. Piel leg.; 2 males, Jiangxi Prov.; 1 male, Zhenba County (32° 30'N, 107° 54'E), Shanxi Prov., 20.vii.1985, S. Z. Ren leg.

Description. - Dark brown, female paler than male, with long and sparse brown hairs. Head dark brown, jugs faintly reddish; antennal segment I, IV and extreme base of II dark brown; II brown, gradually turned into dark brown or black apically; III and extreme base of IV yellowish brown. Rostrum surpassing the hind coxae slightly. Collar dirty dark brown, slightly thinner than the basal diameter of antennal segment II, with a row of long black hairs. Pronotum shiny brown, with a darker broad medial longitudinal stripe, sometimes completely dark brown or black (especially the males), or completely brown (especially the females), slightly wrinkled transversely, calli smooth. Scutellum dark brown to black, slightly convex, finely wrinkled transversely, with a transverse impression before extreme apex; pubescence sparse, brown. Mem-

brane dirty black. Legs dark brown, tibial spines shorter than the tibial diameter. Thoracic ventral surface dull, dirty black, hairless. Venter shiny, unevenly reddish brown, male pygofer with a long knob (length 0.33) before left clasper (fig. 6). Vesica with 3 shagreened membranous lobes, an elongate sclerotized plate, connected with a flossy membranous lobe topped with dense minute hairs (figs. 9, 10); left clasper much longer than the right one (figs. 6-8).

Measurements: Body length 8.56-10.09, width 2.93-3.30; head apex to cuneal suture 6.14-7.70. Head length male 1.32-1.35, female 1.27-1.32; width male 1.35-1.39, female 1.35-1.42. Vertex width male 0.39-0.40, female 0.51-0.52. Antennal segment lengths male 1.32-1.40 : 3.42-3.68 : 2.41-2.58 : 1.20-1.29, female 1.31-1.42 : 3.65-3.95 : 2.61-2.81 : 1.47-1.61. Rostrum length 3.75-3.89. Pronotum length 1.57-1.68, width 2.55-2.91. Scutellum length 1.40-1.47. Corium length 4.36-4.69. Length of anterior femur : tibia : tarsus = 2.34-2.42 : 2.75-2.93 : 0.74-0.82; length of hind femur : tibia : tarsus = 2.89-4.15 : 6.03-6.70 : 0.70-1.04.

Remarks. – *M. pronotalis* differs from other known species in the large size, characteristic markings on the pronotum, long and sparse hairs, and the structure of genitalia.

2. *Megacoelum chinensis* sp. n. (figs. 11-17)

Type material. – Holotype: Male, Sangang (27°42'N, 117°36'E), Chong'an County, Fujian Prov., 22.vi.1965, L. C. Wang leg. – Paratypes: 3 males, 3 females, with same locality as holotype, 22/23.vi.1965; 3 males, 8 females, with same locality as holotype, 20.vii./8.viii.1982, H. G. Zou et al leg.; 2 males, Guadun (26°42'N, 117°36'E), Chong'an County, Fujian Prov., 6.viii.1982, C. Chen & P. P. Chen leg.; 1 male (TJNM), Aotou (27°18'N, 118°6'E), Jianyang County, Fujian Prov., 21.vi.1965, S. L. Liu leg.; 1 male (TJNM), Mt. Tianmu (30°24'N, 119°30'), Zhejiang Prov., 15.viii.1965, S. L. Liu leg.; 1 male (TJNM), with same data as holotype, S. L. Liu leg.

Description. – Body relatively short and broad, dark brown to black. Head dull, unevenly brownish black. Antennal segment I thickest, brown, ventral surface darker, with several black setae on inner surface; II brown, slightly incrassate and darkened into black apically, extreme base black; III and IV reddish brown, with paler extreme base, as thick as the base of II. Collar dirty black, slightly thinner than the basal diameter of antennal segment II, with a row of elongate and slender pale hairs. Pronotum shiny, black with pale sparse elongate pubescence, wrinkled transversely, calli smooth. Scutellum slightly convex, densely and finely wrinkled transversely. Hemelytra with sparse long

pale pubescence, membrane smoky black. Legs brown, apical 1/6 of femora darker, hind tibiae dark brown. Thoracic ventral surface dirty dark brown. Venter reddish brown, male pygofer with a very short knob before left clasper. Vesica with 4 large membranous lobes, two of which with apical fine shagreened teeth (fig. 16), a slender rod-like sclerotized spicule curved before apex (fig. 17), and an angulate lobe densely and strongly shagreened (fig. 15). Left clasper (figs. 11-13) long and curved, right clasper short and thick (fig. 14).

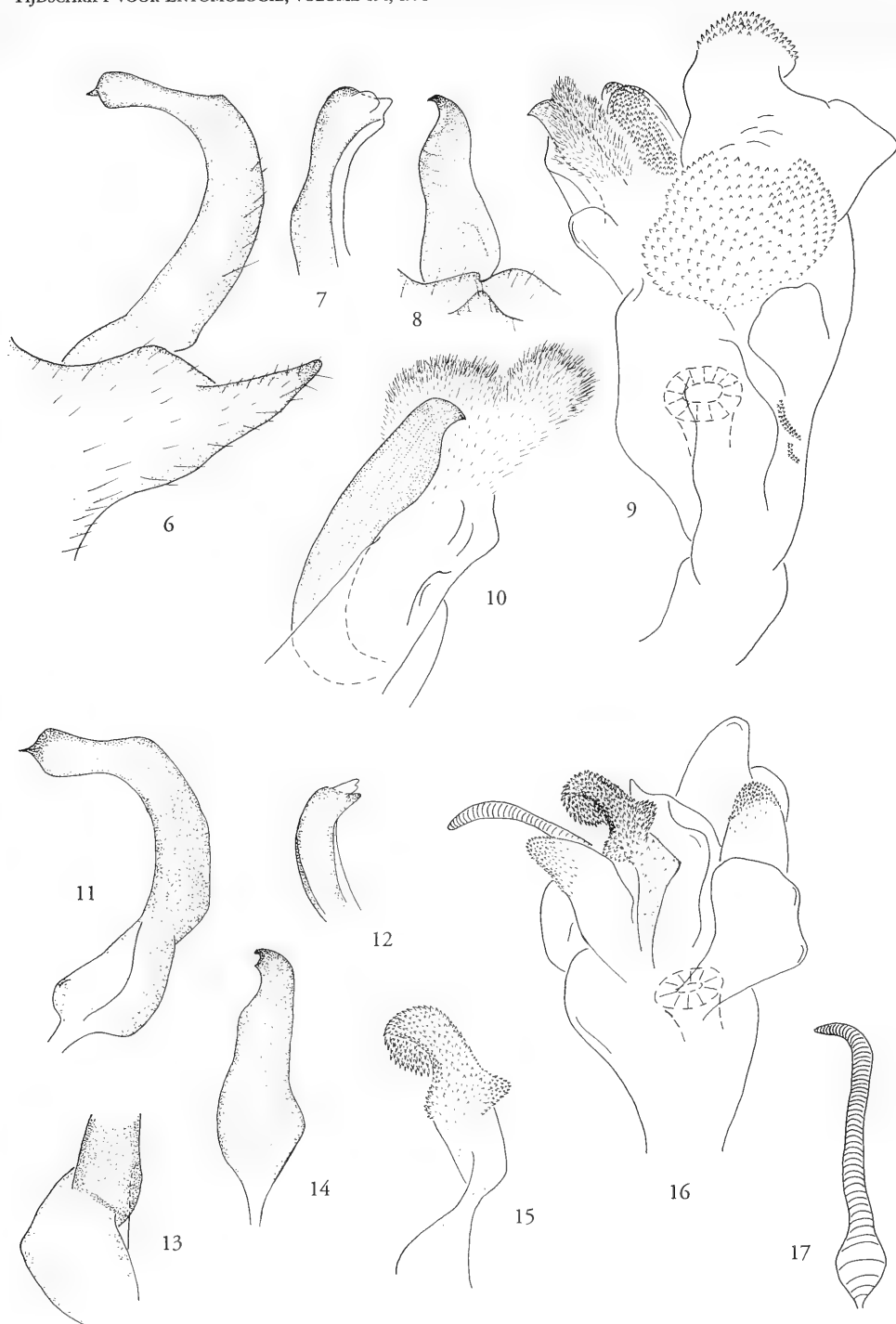
Measurements: Body length 6.88-8.74, width 2.48-3.15; head apex to cuneal suture 5.12-6.75. Head length 1.09-1.16, width 1.20-1.32. Vertex width male 0.46-0.50, female 0.49-0.50. Antennal segment lengths 1.21-1.42 : 3.02-3.35 : 2.28-2.68 : 1.21-1.41. Rostrum length 3.15-3.38. Pronotum length 1.27-1.44, width 2.08-2.48. Scutellum length 1.01-1.17, width 1.07-1.24. Corium length 3.45-4.22. Length of anterior femur : tibia : tarsus = 1.68-2.09 : 2.41-2.65 : 0.65-0.67, length of hind femur : tibia : tarsus = 3.08-3.80 : 4.86-5.43 : 0.67-0.78.

Remarks. – Body shape and colour somewhat similar to *M. pronotalis* sp. n., but differs in smaller size, longer pubescence and the different structure of male genitalia.

3. *Megacoelum rubripedum* sp. n. (figs. 19-25)

Type material. – Holotype male: Sangang (27°42'N, 117°36'E), Chong'an County, Fujian Prov., 5.viii.1982, H. G. Zou leg. – Paratypes: 3 males, 2 females, with same locality as holotype, 29.vii./7.viii.1982, C. Chen et al leg.; 5 males, 2 females, Hexi (24°48'N, 117°12'E), Nanjing County, Fujian Prov., 22.vii.1965, L. C. Wang leg.

Description. – Reddish black, sometimes the female slightly paler, with dense and short yellowish brown hairs. Head dark brown, dull, antennae slender and elongate, red to brown, extreme base of segment II black, extreme base of III, extreme base and apex of IV yellowish brown. Collar brown, thinner than the basal diameter of antennal segment II, with a row of elongate hairs with swollen base. Pronotum black, basal margin narrowly brownish red, densely and transversely wrinkled, calli indistinct. Scutellum black, with fine and dense transverse wrinkles. Hemelytra black, embolium and cuneus brown to red; membrane smoky black, apical angle of large cell nearly rectangular. Legs reddish brown to red. Thoracic ventral surface including coxae dull black. Venter unevenly brownish black, with sparse brown hairs. Male pygofer without any knob before left clasper. Vesica (fig. 22) with 4 membranous lobes (one of them strongly



Figs. 6-17. *Megacoelum* spp. – 6, 7, *Megacoelum pronotalis* sp. n., left clasper; 8, idem, right clasper; 9, idem, vesica in dorsal view; 10, idem, vesica, sclerotized plate and flossy membranous lobe, ventral view; – 11-13, *Megacoelum chinensis* sp. n., left clasper; 14, idem, right clasper; 15, idem, vesica in dorsal view; 16, idem, vesica, shagreened lobe; 17, idem, vesica, spicule.

and roughly shagreened apically, as fig. 24) and dorso-medially a mushroom-like appendage with a sclerotized cap-shaped apex (figs. 23, 25). Left clasper elongate and curved (figs. 18-20), right clasper short, broadly toothed medially (fig. 21).

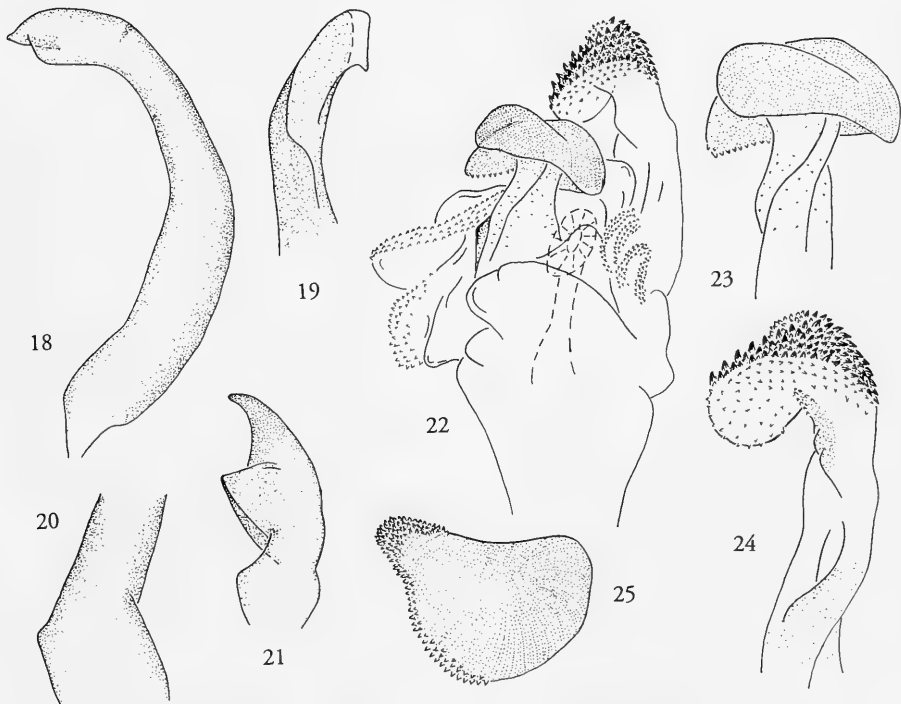
Measurements: Body length 5.81-7.63, width 2.05-2.68; head apex to cuneal suture 4.37-6.03. Head length 0.99-1.22, width 1.09-1.32. Vertex width male 0.43-0.45, female 0.41-0.51. Antennal segment lengths 1.11-1.51 : 2.60-3.75 : 2.28-3.02 : 1.17-1.41. Rostrum length 3.28-3.35. Pronotum length 1.10-1.40, width 1.80-2.21. Scutellum length 0.90-1.21, width 0.90-1.21. Corium length 2.93-3.82. Length of anterior femur : tibia : tarsus = 1.58-1.89 : 1.91-2.48 : 0.54-0.63, length of hind femur : tibia : tarsus = 2.75-3.52 : 4.14-5.26 : 0.59-0.76.

Remarks. – Differs from other known species in the slender and elongate antennae, red or reddish brown legs, dense and short pubescence and the structure of male genitalia.

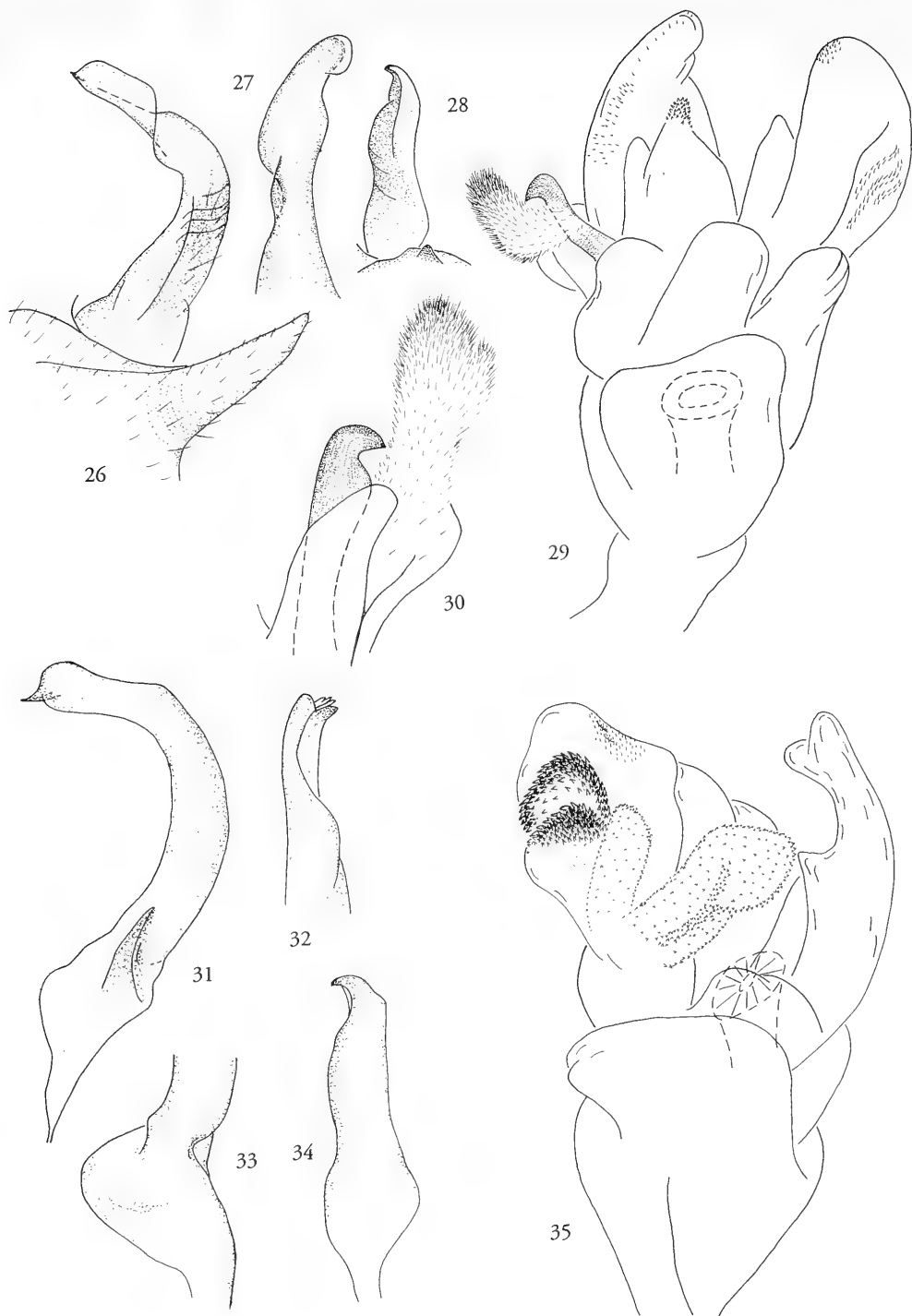
4. *Megacoelum pseudopronotalis* sp. n. (figs. 26-30)

Type material. – Holotype male: Yanshan (27° 18' N, 117° 18' E), Shaowu County, Fujian Prov., 28.v.1965, L. C. Wang leg. – Paratypes: 1 male, with same data as holotype; 1 male (TJNM), Sangang (27° 42' N, 117° 36' E), Chong'an County, Fujian Prov., 22.vi.1965, S. L. Liu leg.

Description. – Black or reddish brown, with sparse dark brown hairs. Head dark brown to black, weakly shining. Gula horizontal. Antennal segment I, extreme base of II black; basal half of II yellowish brown, III and IV absent. Collar dull, black, as thick as the basal diameter of antennal segment II, with a row of elongate dark hairs. Pronotum black, shiny, pubescence sparse, weakly wrinkled transversely, calli smooth with margins indistinct. Scutellum shiny black, finely and transversely wrinkled. Hemelytra dark reddish brown, membrane smoky black. Legs brownish black, an-



Figs. 18-25, *Megacoelum rubripedum* sp. n. – 18-20, left clasper; 21, right clasper; 22, vesica in dorsal view; 23, vesica, lateral view of mushroom-like lobe; 24, same, top view; 25, vesica, shagreened lobe.



Figs. 26-35, *Megacoelum* spp. – 26, 27, *Megacoelum pseudopronotalis* sp. n., left clasper; 28, idem, right clasper; 29, idem, vesica in dorsal view; 30, idem, vesica, sclerotized plate and flossy membranous lobe; 31-33, *Megacoelum zoui* sp. n., left clasper; 34, idem, right clasper; 35, idem, vesica, dorsal view.

terior and middle tibiae excepting extreme apex brown. Thoracic ventral surface dull, black. Venter brownish black. Knob on pygofer before left clasper in male large and sharp, length 0.39 (fig. 26). Vesica (fig. 29) very similar to that of *M. pronotalis* sp. n., but the sclerotized plate more strongly hooked apically (figs. 29, 30). Apical 1/3 of the left clasper (figs. 26, 27) twisted. Right clasper (fig. 28) close to that of *M. pronotalis* sp. n.

Measurements: Body length 8.37-8.56, width 2.75-2.80; head apex to cuneal suture 5.91-6.14. Head length 1.24-1.25, width 1.34-1.35. Vertex width 0.46-0.48. Lengths of antennal segment I and II = 1.34-1.35 : 3.35-3.75. Rostrum length 3.73-3.76. Pronotum length 1.38-1.39, width 2.41-2.43. Scutellum length 1.16-1.22, width 1.29-1.32. Corium length 4.00-4.09. Length of anterior femur : tibia : tarsus = 2.18-2.21 : 2.61-2.66 : 0.70-0.72, length of hind femur : tibia : tarsus = 2.69-2.75 : 5.70-5.90 : 0.80-0.81.

Remarks. – Closely allied to *M. pronotalis* sp. n. in the body size and shape, but the pronotum always black, the structure of vesica and the left clasper different.

5. *Megacoelum zoui* sp. n. (figs. 31-35)

Type material. – Holotype, male, Mengxiu, Ruili County (24°0'N, 97°48'E), Yunnan Prov., 3.ix.1979, H. G. Zou leg. – Paratypes: 1 male, 1 female, with same locality as holotype, 2.ix.1979, J. X. Cui and G. Q. Liu leg.

Description. – Dark brown, weakly shiny with very dense and short brown pubescence. Head blackish brown, clypeus slightly convex; antennal segment I, extreme base of II and the apical parts of III and IV dark brown, darkened apically, bases of III and IV yellowish brown. Collar brown, median part black, thinner than the basal diameter of antennal segment II. Pronotum medially with a vague longitudinal black stripe. Scutellum convex, black or dark brown, extreme apex brown. Membrane smoky black, veins black. Front legs brown, with darker femora; middle femora and the basal half of tibia dark brown; hind leg reddish black. Thoracic ventral surface dark brown. Venter dark reddish with brown hairs. Knob on pygofer before left clasper in male small. Vesica (fig. 35) with 4 membranous lobes, one of them strongly and densely toothed apically. Left clasper (figs. 31-33) long and curved, right one (fig. 34) short and straight.

Measurements: Body length 7.81-8.37, width 2.61-2.79; head apex to cuneal suture 5.57-5.59. Head length 1.09-1.14; width male 1.25-1.27, female 1.25. Vertex width male 0.43-0.46, female

0.46. Antennal segment lengths 1.14-1.31 : 3.08-3.35 : 2.27-2.51 : 1.17-1.21. Rostrum length 3.35-3.72. Pronotum length 1.30-1.32, width 2.25-2.31. Scutellum length 1.12-1.22, width 1.13-1.26. Corium length 3.58-3.86. Length of anterior femur : tibia : tarsus = 2.01-2.11 : 2.55-2.58 : 0.60-0.67, length of hind femur : tibia : tarsus = 3.15-3.25 : 5.16-5.49 : 0.70-0.80.

Remarks. – This species is distinguished from the others in the dense and short pubescence, the vague longitudinal dark stripe running from pronotum to scutellum, and the structure of male genitalia.

6. *Megacoelum tenuicorne* sp. n. (figs. 36-40)

Type material. – Holotype male, Canton (23°6'N, 113°12'E), Guangdong Prov. – Paratypes: 12 males, 2 females, with same data as holotype; 1 male, 4 females, Baoxing (30°18'N, 102°49'E), alt. 950-1360m, Sichuan Prov., 16/18.vi.1963, L. Y. Zheng and H. G. Zou leg.; 1 female, Mt. Emei (29°30'N, 103°18'E), alt. 600m, Sichuan Prov., 4.vi.1957, L. Y. Zheng and H. H. Cheng leg.; 1 male (TJNM), Jinchuan (31°27'N, 102°0'E), alt. 2000-2300m, Sichuan Prov., 10.ix.1963, S. L. Siu leg.; 1 male, 1 female (TJNM), Cuijiang (25°42'N, 102°0'E), Longsheng County, Guangxi Prov., 24/25.viii.1964, S. L. Liu leg.

Description. – Reddish brown, pubescence sparse, elongate and pale. Female larger than male. Clypeus prominent, frons with fine red transverse stripes at lateral sides; antennae thin and brown, segment I with a brown seta on inner margin; rostrum surpassing hind coxae. Collar brown, with a row of long hairs, slightly thicker than the basal diameter of antennal segment II. Pronotum shiny, smooth, posterior lobe indistinctly wrinkled, basal margin slightly raised; calli somewhat reddish. Scutellum weakly but densely wrinkled, slightly convex. Hemelytra sometimes mottled with some red spots, outer part of corium, embolium and outer part of cuneus semi-transparent, membrane smoky black. Legs brown, apical halves of middle and hind femora, apical 3/4 of middle and hind tibiae reddish brown, tarsi dark. Thoracic ventral surface dull, brown. Venter red. The knob before left clasper in male distinct (fig. 37). Vesica (fig. 36) with 5 membranous lobes, most of them shagreened or toothed, one of them with flossy apex. Left clasper elongate, thin and curved (figs. 37-39), right clasper as in fig. 40.

Measurements: Body length male 6.46-7.00, female 6.95-7.39; width male 2.11-2.48, female 2.42-2.60; head apex to cuneal suture male 4.76-5.13, female 5.07-5.39. Head length 1.05-1.09, width 1.14-1.16. Vertex width male 0.36-0.40, female 0.44-0.66. Antennal segment lengths 1.01-1.17 : 2.95-3.55 : 2.39-2.81 : 1.16-1.41. Rostrum length

3.08-3.62. Pronotum length male 1.12-1.16, female 1.22-1.24; width male 1.84-1.95, female 1.98-2.15. Scutellum length male 0.89-0.96, female 0.92-1.02; width male 0.89-1.02, female 0.99-1.24. Corium length male 3.42-3.49, female 3.72-3.86. Length of anterior femur : tibia : tarsus = 1.84-1.98 : 2.41-

2.52 : 0.63-0.68; length of hind femur : tibia : tarsus = male 2.95-3.02 : 4.59-4.84 : 0.70-0.74, female 3.06-3.18 : 5.03-5.36 : 0.73-0.78.

Remarks. - Differs from other species in the slender antennae and the structure of male genitalia.



Figs. 36-45, *Megacoelum* spp. - 36, *Megacoelum tenuicorne* sp. n., dorsal view of vesica; 37-39, idem, left clasper; 40, idem, right clasper; 41, *Megacoelum yunnanum* sp. n., right clasper; 42, 43, idem, right clasper; 44, idem, vesica in dorsal view; 45, idem, vesica, sclerotized broad plate, ventral view.

7. *Megacoelum yunnanum* sp. n.

(figs. 41-45)

Type material. – Holotype male, Mengla (21°24'N, 101°30'), Yunnan Prov., 24.ix.1979.

Description. – Dark brown, with very dense and short pubescence on the hemelytra. Head dull, brown, antennae brown, subbasal part of segment II and basal 1/3 of III yellowish, IV absent. Collar brown, thinner than the basal diameter of antennal segment II. Pronotum black, basal margin narrowly yellow and slightly reflexed; calli and the area before and behind dark reddish brown; deeply, densely and transversely wrinkled excepting the smooth calli. Scutellum convex, black, lateral angles slightly paler, with fine transverse wrinkles. Hemelytra black with dense and short pubescence, hind part of embolium and outer margin of cuneus reddish, apical 1/3 of cuneus yellowish brown, membrane smoky black. Legs pale brown, apices of anterior and median tibia dark brown. Thoracic ventral surface brown, with black stripes, coxae black. Anterior part of venter reddish brown, posterior part black. The knob on pygofer before left clasper in male short (fig. 42). Vesica (fig. 44) with 5 membranous lobes, the ventral surface of the right one sclerotized into a broad plate with its broad knob-like apex bending sideward and armed with numerous minute teeth (fig. 45); the median one with a slender and shagreened (or minutely toothed) shaft and a widened round apex, the latter armed with numerous strong spines directing ventrad (fig. 44). Left clasper as figs. 42 and 43, right clasper as fig. 41.

Measurements: Body length 67.6, width 2.33; head apex to cuneal suture 5.3. Head length 1.02, width 1.16. Vertex width 0.41. Antennal segment lengths = 1.17 : 2.95 : 1.88 : ?. Pronotum length 1.40, width 2.25. Scutellum length 1.07, width 1.15. Corium length 3.52. Length of anterior femur : tibia : tarsus = 1.88 : 2.17 : 0.60; length of posterior femur : tibia : tarsus = 2.30 : 2.84 : 0.61.

Remarks. – The narrowly yellow and reflexed pronotal basal margin, deeply and transversely wrinkled disk of pronotum, dense and short hemelytral pubescence distinctly distinguish this new species from other members of the genus.

8. *Megacoelum fuscescens* Hsiao, 1963

(figs. 1-5)

Megacoelum fuscescens Hsiao, 1963: 440, 442-443, 448; figs. 1a, 2a, 3. Holotype ♂: Xishuangbanna-Xiaomen-gyang (22°0'N, 100°48'E), Yunnan Prov., 24.viii.1958 (in Institute of Zoology, Academia Sinica, Beijing) [examined].

Description. – Dark brown, mottled with lighter hue, with sparse, fine, long and greyish hairs. Head brown, eyes black, frons with several oblique stripes on both sides. Antennal segment I, most of IV, and apical 1/4 of II dark brown; III, basal 3/4 of II, extreme base of IV yellowish brown, sometimes extreme base and middle of II dark brown; I with sparse hairs, II to IV with black setae, II with moderately sparse and long hairs, III and IV with short and dense hairs. Rostrum reaching the apex of hind coxae. Collar opaque, pale yellowish brown or dark brown, slightly thinner than the basal diameter of antennal segment II, with a row of long greyish hairs and some pale soft hairs. Pronotum shiny, dark brown, lateral margins and basal part nearly black, extreme basal margin yellowish brown; calli distinctly smooth, reaching antero-lateral angles; posterior pronotal lobe obscurely wrinkled transversely; basal margin slightly curved posterad. Scutellum dark brown, opaque, relatively flat, finely and transversely wrinkled. Hemelytra dark brown, membrane dark. Legs brown, sometimes with dark spots; middle femora and tarsus dark, tibial spine shorter than tibial diameter. Thoracic ventral surface and coxae dull, dark brown. Venter shiny dark brown, sometimes with brown spots, male pygofer with a short knob before left clasper. Vesica with 4 large membranous lobes, among them arised a spicule, slightly flattened and curved dorsally (figs. 1 and 2). Base of left clasper moderately thick, curved and tapered apically (figs. 3 and 4). Right clasper as in fig. 5.

Measurements: Body length 6.8-7.4, width 2.2-2.4; head apex to cuneal suture male 5.2-5.3, female 4.7-4.9. Head length male 1.09, female 1.06-1.07; width male 1.22, female 1.16-1.17. Vertex width male 0.32, female 0.35-0.36. Lengths of antennal segment = male 1.20-1.28 : 2.93-3.15 : 2.67-2.73 : 1.28-1.32, female 1.17-1.19 : 2.68-2.90 : 2.48-2.74 : 1.21-1.29. Rostrum length 3.2. Pronotum length male 1.18-1.43, female 1.12-1.13; width male 1.95-2.14, female 1.90-1.98. Scutellum length 0.99-1.07, width 1.03-1.15. Corium length 3.43-3.59. Length of anterior femur : tibia : tarsus = 1.98 : 2.36 : 0.62; length of hind femur : tibia : tarsus = 3.22-3.35 : 5.03-5.39 : 0.77.

Remarks. – Hsiao & Meng (1963) remarked that this species is 'possibly allied to *M. straminipes* Dist. from India but the first antennal segment shorter, corium concolorously fuscous and apical fourth of posterior femora black'. The species differs from others in the structure of male genitalia.

Material examined. – 1 male, holotype; 2 males, Ruili (24°0'N, 97°48'E), Yunnan Prov., 28/31.viii.1979, Z. P. Ling and J.X. Cui leg.; 3 males, Lianxian County

(24° 42' N, 112° 18' E), Guangdong Prov., 20/24.ix.1962, L. Y. Zheng and H. H. Cheng leg., on Gramineae and *Capsium frutescens* L.; 1 male, 2 females, Longzhou County (22° 18' N, 106° 48' E), Guangxi Prov., 13/18.vii.1964, L. C. Wang leg.; 4 males, 4 females (TJNM), Longzhou County, Guangxi Prov., 15/21.vii.1964, S. L. Liu leg.; 1 female (TJNM), Jianfengling (18° 42' N, 108° 48' E), Hainan Prov., 10.v.1964, S. L. Liu leg.

9. *Megacoelum clypeale* Poppius, 1915

Megacoelum clypeale Poppius, 1915: 14-15. Holotype female: [Taiwan] Kosempo, X, (Deutschen Entomologischen Museum, Berlin) [not examined].

10. *Megacoelum minutum* Poppius, 1915

Megacoelum minutum Poppius, 1915: 15. Holotype male: [Taiwan], Takao, 18.vii.1907, (Universitäts-Museum, Helsingfors) [not examined].

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RELATIONSHIPS OF THE GENUS *HETEROCHEILA* (DIPTERA: SCIOMYZOIDEA) WITH DESCRIPTION OF A NEW FAMILY

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A morphological comparison is made of the maritime kelp-living genus *Heterocheila* Rondani with the families of Sciomyzoidea, particularly the Helcomyzidae. It is concluded that it has no particularly close relationship with any one of these families, and the new family Heterocheilidae (halfbridge flies) is established for it. *Heteromyza orientalis* Macquart, 1843 is a new synonym of *Heterocheila buccata* (Fallén, 1820).

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Key words. – Diptera; Heterocheilidae, new family; Holarctic.

In the course of my recent work on the Coelopidae (kelp flies) (D. McAlpine 1991) it became apparent that (1) there is disagreement in recent literature as to the family position of *Heterocheila*, and (2) it is difficult on morphological grounds to justify the inclusion of *Heterocheila* in the various families (Coelopidae, Dryomyzidae, Helcomyzidae) where it has been recently assigned. For these reasons the present investigation was made.

The holarctic genus now known as *Heterocheila* Rondani, 1857, has often been referred to by the synonymous name *Oedoparea* Loew, 1862. See both Steyskal (1965), and Gorodkov (1984) for complete synonymy. Included species are: (1) *H. buccata* (Fallén, 1820) (syn. *Heteromyza orientalis* Macquart, 1843), from Europe; (2) *H. hannai* (Cole, 1921) (syn. *H. nudiseta* Curran, 1933), from Pacific North America. Both species live in stranded kelp (see especially Egglshaw 1960b).

Heterocheila (or *Oedoparea*) has often been placed in the family Helcomyzidae (e.g. Malloch 1933; Hennig 1937, 1973; Steyskal, 1958, 1965; Gorodkov 1984), or in the Dryomyzidae, broadly defined to include *Helcomyza* Curtis and allied genera (e.g. Czerny 1930; Steyskal 1987; J. McAlpine 1989). Egglshaw (1960b), Dobson (1976), and Griffiths (1972) have preferred to place *Heterocheila* in the Coelopidae (with some reservations), but I have given definite reasons for its exclusion from the Coelopidae (D. McAlpine 1991), and these need not be repeated here.

Useful descriptive and illustrative material of the adult morphology of *Heterocheila* has been given by Czerny (1930), Hennig (1958), Steyskal (1958, 1962, 1987), and Griffiths (1972). Backlund (1945) and Egglshaw (1960b) have described the egg, larva and puparium of *Heterocheila*, and the latter also gives important biological information. I have examined a series of adults of both sexes of *H. buccata*, and collected the species in the field. W. N. Mathis has provided material of *H. hannai*.

The family Helcomyzidae is here considered to include only the genera *Helcomyza* Curtis, *Maoriomyia* Tonnoir & Malloch, and *Paractora* Bigot. I have given reasons for excluding the group from the Dryomyzidae (D. McAlpine 1991) and suggested a closer relationship to the Coelopidae. Useful descriptive and illustrative material of the adult morphology of Helcomyzidae has been given in most of the papers mentioned above for *Heterocheila* morphology, also by Malloch (1933). Egglshaw (1960a) has described the larva and puparium of *Helcomyza*, and given biological information. I have examined adult material of all genera and most described species of Helcomyzidae.

In the following text I use the superfamily Sciomyzoidea to include the families Sciomyzidae, Huttoninidae, Helosciomyzidae, Dryomyzidae, Helcomyzidae, Coelopidae, Ropalomeridae, Sepsidae, Chamaemyiidae (including Cremifaniidae), Eurychoromyiidae (probably excluding the *Gayomyia* complex, see J. McAlpine 1989), and Laux-

aniidae (including Celyphidae). J. McAlpine (1989) includes the last three families in a separate superfamily Lauxanioidea.

SIMILARITIES OF HETEROCHEILA TO HELCOMYZIDAE

Heterocheila shares with Helcomyzidae s. str. the beach habitat and dependence on stranded kelp, utilising it for larval nutrition as well as shelter. These habits are shared with a number of other Diptera, notably the Coelopidae, the sepsid genus *Orygma* Meigen, and the sphaerocerid genus (or subgenus) *Thoracochaeta* Duda. Similarity of habits and habitat seems to have caused some convergent similarities among these shoreline flies, so that *Orygma* and *Heterocheila* have been referred to the Coelopidae in the past.

In elevating Helcomyzidae to family status, Malloch (1933) emphasised the significance of the sclerotised precoxal bridge, which connects the prosternum to the propleuron on each side. Hennig (1958) considered this condition to represent a synapomorphy peculiar to the Helcomyzidae plus Ropalomeridae among the Schizophora, which he therefore considered to constitute a monophyletic group. It is now known that prothoracic precoxal bridges occur in at least some representatives of at least 19 schizophoran families (Speight 1969, and my observations), and many arisals of the condition are acknowledged. Within the superfamily Sciomyzoidea, the trait occurs also in some sciomyzids as an independent apomorphy. The presence of precoxal bridges is not now usually considered as proof for monophyly of Helcomyzidae and Ropalomeridae (Griffiths 1972; J. McAlpine 1989), and additional evidence is needed if monophyly of *Heterocheila* with Helcomyzidae is to be established. The precoxal bridge in *Heterocheila* differs somewhat from that of Helcomyzidae in being markedly narrower.

In both *Helcomyza* and *Heterocheila* the basal crossvein (crossvein bm-cu or base of M_{3+4} according to divergent applications of the Comstock-Needham notation) lies more obliquely, with approach to a longitudinal orientation, than in *Dryomyza*. This condition is unlikely to be a groundplan condition for Helcomyzidae s. str. in view of the fact that the undoubted helcomyzid *Maorimyza* has the basal crossvein more nearly transverse than in four available *Dryomyza* species. I also find some variation in this character in both Coelopidae and Sciomyzidae. It appears to be a rather unsatisfactory indicator of phylogenetic affinities in the Sciomyzoidea.

Heterocheila, *Maorimyza*, and *Helcomyza* have two spermathecae in the female abdomen, as dis-

tinct from the investigated dryomyzids and the apparent groundplan of Coelopidae. On the other hand the number of spermathecae is unrecorded for the helcomyzid genus *Paractora*.

Increasing knowledge of spermathecal numbers in Schizophora has demonstrated that it is a fairly unstable character. The change from three to two spermathecae must have happened many times in the evolution of the Schizophora, if, in fact, the change has always been in the one direction. In the Sciomyzoidea, variation in spermathecal number occurs within the families Huttoninidae, Coelopidae, and Sciomyzidae.

Other traits shared between *Heterocheila* and the Helcomyzidae are, so far as I am aware, found in a wide spectrum of sciomyzoid flies and have not been postulated as evidence of closer relationship between these two taxa. Such traits include the development of mollisetae (see D. McAlpine 1991) on various parts of the males, the general brownish grey pruinulent covering of the cuticle, characteristic of many shore-dwelling flies, and the shining parafacial ridges, also found in many flies of maritime or sandy habitats.

DIFFERENCES BETWEEN HETEROCHEILA AND HELCOMYZIDAE

The principal morphological differences between adults of these taxa are given in table 1. They are discussed below in numerical sequence, with the addition of some comments on larval morphology (18).

1. Hackman & Väisänen (1985) have investigated the costal chaetotaxy of the Diptera (including *Heterocheila*, op. cit.: fig. 16) and assigned it some taxonomic value at the family and subfamily levels. The additional dorsal and ventral rows of costal setulae present in *Heterocheila* are in agreement with Dryomyzidae and Helosciomyzidae (but not *Coelopa frigida* (Fabricius) with which Hackman & Väisänen compare it). The absence of these series in all genera of Helcomyzidae is in contrast to the above taxa. The presence of outstanding anteroventral spines at intervals on the mid region of the costa in all Helcomyzidae separates them sharply from the Dryomyzidae and *Heterocheila*, and aligns them with Helosciomyzidae and some Coelopidae (e. g. *Lopa convexa* McAlpine, *Gluma keyzeri* McAlpine, and *Rhis whiteleyi* McAlpine, see D. McAlpine 1991).

2. The discontinuity of the parafacial suture on its lower part and peculiar angular shining parafacial ridge are apparently autapomorphies of the Helcomyzidae. The condition in *Heterocheila* is probably partly plesiomorphic, though the extensive shining ridge may be an autapomorphy.

3. The incised, vertically orientated postgenal fold in *Heterocheila*, is an unusual feature in the Sciomizoidea and presumably an autapomorphy. A similar condition occurs in the heleomyzid *Nephelium dendrophilum* (Malloch) (D. McAlpine 1985: Fig. 30).

4. The Helcomyzidae share with the Helosciomyzidae the narrow median emargination of the face adapted to receive the prelabrum. The emargination is absent in *Heterocheila* and Dryomyzidae, but a somewhat similar emargination occurs in some, Coelopidae, though it is doubtful if it is in the groundplan of the latter. Perhaps the median emargination represents a separate apomorphy in each group in which it occurs.

5. The shape of the hypopleural channel in the Helcomyzidae represents a distinctive autapomorphy, absent in *Heterocheila* (D. McAlpine 1991: Fig. 9).

6. The significance of this character has been discussed above under 'Similarities'.

7. The male-restricted apical ventral process of the fore basitarsus is a trait difficult to evaluate phylogenetically, possibly because of irregular loss in a number of lineages (D. McAlpine 1991). In the Sciomizoidea it is apparently restricted to Helcomyzidae, Coelopidae, and Dryomyzidae, though not uniformly present in the last family. It does not appear to be a synapomorphy as it also occurs in a number of Heleomyzoidea and in *Heloclusia imperfecta* Malloch, a somewhat primitive representative of the Neriioidea. This condition seems unlikely to have originated more than once. I therefore regard it as a very ancient trait and it may provide evidence for relationship between Sciomizoidea, Heleomyzoidea, and Neriioidea. In this case, its absence in *Heterocheila* would be a derived state, but not necessarily a synapomorphy with other sciomyzoids in which it is also absent.

8. The phylogenetic significance of the reduction of tergite 6 of the male abdomen in Sciomizoidea does not appear to have been satisfactorily explained. J. McAlpine (1989) regards reduction of tergite 6 as a groundplan apomorphy of his Sciomizoidea (as distinct from Lauxanioidea) but includes in Sciomizoidea such taxa as *Heterocheila*, *Orygma* Meigen (Sepsidae), and *Rhytidops* Lindner (Ropalomeridae) which have a large (and in *Orygma*, according to J. McAlpine, primarily unreduced) tergite 6. For this and other reasons, I include the lauxanioid families Chamaemyiidae, Lauxaniidae, and Eurychoromyiidae in the Sciomizoidea.

If evolutionary change in the size of tergite 6 takes place only in the direction of reduction, this might seem to support the idea of a monophyletic group including Dryomyzidae, Helcomyzidae, Coe-

lopidae, and perhaps other families, but excluding *Heterocheila*, Ropalomeridae, Sepsidae, Chamaemyiidae, Lauxaniidae and Eurychoromyiidae. Convergence in this character cannot be excluded, but seems less likely for the complex Dryomyzidae plus Helcomyzidae plus Coelopidae, plus perhaps Helosciomyzidae, as these families show several other somewhat inconsistent similarities. Thus, the size of tergite 6 in *Heterocheila* makes difficulties for the hypothesis that it is close to the Helcomyzidae or Coelopidae.

9. The aedeagus of Helcomyzidae is more similar to that of Dryomyzidae than to that of *Heterocheila* (Griffiths 1972). My study of the aedeagus in Coelopidae (D. McAlpine 1991) and Heleomyzidae (e. g. D. McAlpine 1967) shows that its structure may be quite unstable above the species level.

There are apparently consistent differences in both hypandrium and aedeagus between *Heterocheila* and Helcomyzidae. The hypandrium of *Heterocheila* has two pairs of processes posteriorly (gonites or parameres) which are absent in helcomyzids. The aedeagus of *Heterocheila* has a pair of spreading lateral lobes at the junction of the basiphallus and distiphallus, which is absent in the helcomyzids examined, but it lacks the patch of pubescence near the middle of the length of the distiphallus, which is present in helcomyzids.

Griffiths (1972) has emphasised the substantial differences in external male genitalia between *Heterocheila* and certain helcomyzids. It is possible that these structures should be assigned relatively low reliability as indicators of relationship. To judge from my studies of the Heleomyzidae (D. McAlpine 1967, 1985) and the Coelopidae, the copulatory structures are so unstable above species level that it is difficult to homologue the various processes and lobes across the family. Therefore there is little logic in inferring autapomorphies between special conditions of certain coelopids and those occurring in *Heterocheila*, which is certainly not so close as a sister group to the Coelopidae. However, I find greater consistency in hypandrial structure within the smaller taxonomic diversity of the Helcomyzidae.

10. The presence of a female-restricted enlarged, isolated, posteriorly directed bristle on each lateral margin of tergites 2 to 4 and sometimes 5 is characteristic for most helcomyzids, including species in all 3 genera. It is absent in the Dryomyzidae, but the presence of similar female-restricted bristles in two rather plesiomorphic but not closely related coelopid species (D. McAlpine 1991) may indicate that it was present in the common ancestor of Helcomyzidae and Coelopidae.

11-17. I do not rate these differences in chaetotaxy very highly, taken individually. Collectively,

Table 1. Differences between Helcomyzidae and *Heterocheila* (adults).

Helcomyzidae	<i>Heterocheila</i>
1. Mid region of costa with spaced anteroventral spines, without continuous series of dorsal and ventral setulae.	Mid region of costa without anteroventral spines, with regular series of dorsal and ventral (as distinct from anterodorsal and anteroventral) setulae.
2. Shining parafacial ridge not continued posteriorly below cheek; parafacial suture obsolete or interrupted behind angular section of ridge.	Shining parafacial ridge and associated suture continued below cheek to postgenal region.
3. Postgenal fold absent.	Postgenal fold distinctly incised.
4. Epistomal margin of face with narrow sinuation to receive prelabrum.	Epistomal margin of face without narrow sinuation.
5. Hypopleural channel rather narrow and parallel-sided.	Hypopleural channel expanding rapidly anteriorly.
6. Prothoracic precoxal bridge broad, well sclerotised.	Prothoracic precoxal bridge narrow, not uniformly sclerotised.
7. ♂ fore basitarsus with terminal ventral thumbnail-like process.	♂ (and ♀) fore basitarsus without terminal ventral process.
8. ♂ abdominal tergite 6 much reduced.	♂ abdominal tergite 6 large.
9. Aedeagus with densely pubescent zone or zones, without lateral lobes.	Aedeagus without dense pubescence, with pair of lateral lobes.
10. ♀ with one large bristle near each lateral margin on tergites 2-4.	♀ (and ♂) without lateral marginal bristles on abdominal tergites.
11. Generally only 2 well developed fronto-orbital bristles present.	Fronto-orbital bristles 3.
12. Prostigmatal bristle present (sometimes replaced by several long hairs).	Prostigmatal bristle absent.
13. Median series of acrostichal bristles or setulae not differentiated.	Single regular median series of short acrostichal bristles present (in addition to prescutellar pair).
14. Prosternum setulose.	Prosternum bare.
15. Metasternum setulose.	Metasternum bare.
16. Abdominal sternite 1 setulose.	Abdominal sternite 1 bare.
17. ♀ hind tibia with subapical anterior bristle.	♀ (and ♂) hind tibia without subapical anterior bristle

the seven points indicate a notable degree of divergence between the taxa.

18. Larval morphology of Helcomyzidae is only recorded for *Helcomyza ustulata* Curtis, and it is uncertain if this is representative of the family as a whole. However, in view of the apparently close relationship between the three helcomyzid genera and the very distinctive features of the known larva, these may have some significance for higher classification. According to Egglshaw (1960a, 1960b) the third instar larva of *Heterocheila bucata* has creeping welts of small spines ventrally on

segments 3 or 4 to 12 (no such spinose creeping welts present in *Helcomyza ustulata*, but the cuticle extensively covered with backwardly directed plates), no spine above posterior spiracle (a large spine in this position in *Helcomyza*), each posterior spiracle with two or three groups of short hydrofuge hairs (these absent in *Helcomyza*). There is also difference in the arrangement and spinose armature of the ridges or processes surrounding the anus, and the position of the anus. Egglshaw considers the larvae of *Heterocheila* and *Helcomyza* to be so different that they cannot be-

long in the same family. I am unable to find in his descriptions and figures any shared distinctive traits, which might provide evidence of relatively close relationship between them, though they share many points of resemblance to numerous other schizophoran larvae.

DISCUSSION AND CONCLUSION

The few distinctive points of similarity shared between *Heterocheila* and the family Helcomyzidae are unconvincing as indicators of close phylogenetic relationship. Each of these traits occurs elsewhere in the Sciomyzoidea, and the combination or maritime habitat, a shining section of the parafacial ridge, sclerotised precoxal bridges, and two spermathecae occurs also in the genus *Tethina* Haliday (Chloropoidea: Tethinidae) though this must be only remotely related to Helcomyzidae. It must be acknowledged that convergence between *Heterocheila* and Helcomyzidae in these characters is not an improbable event.

I have indicated a possible sister-group relationship between Coelopidae and Helcomyzidae (D. McAlpine 1991) and this relationship seems to be further supported by costal chaetotaxy. The numerous character differences separating *Heterocheila* and Helcomyzidae indicate a marked evolutionary divergence, and characters 1, 6, 7, 9 and 17 in Table 1 may indicate that *Heterocheila* is probably not to be included in the monophyletic group Helcomyzidae plus Coelopidae, or even the somewhat less surely founded group Dryomyzidae plus Helcomyzidae plus Coelopidae.

Heterocheila resembles at least some taxa of the Ropalomeridae in its sclerotised prothoracic precoxal bridge, large male tergite 6, and two spermathecae. These traits, however, do not provide a stronger case for relationship than those formerly seen to support the now discarded hypothesis of close relationship between Helcomyzidae and Ropalomeridae. *Heterocheila* differs from the Ropalomeridae inter alia in its less markedly divergent postvertical bristles, differently shaped head capsule, unmodified scutellum, absence of setulae on margin of metathoracic spiracle, unmodified femora, and distinct but desclerotised distal section of vein 7. Also *Heterocheila* lives on north-temperate shore-lines, while the ropalomerids are mainly inhabitants of tropical forests of the Americas. Most recent workers (e.g. J. McAlpine 1989) consider the Ropalomeridae to be closely related to the Sepsidae. There is no adequate reason for including *Heterocheila* in this alliance.

Heterocheila also resembles the little known neotropical family Eurychoromyiidae in the prothoracic precoxal bridge, and the latter has an even

larger male tergite 6 (see J. McAlpine 1968, for morphological details). *Heterocheila* lacks the following distinctive characters of Eurychoromyiidae: body form remarkably stout; chaetotaxy greatly reduced; head structure highly modified; antennal segment 1 (scape) elongate; scutellum abbreviated; mesopleural bristles present; tibiae lacking terminal spurs; distal section of vein 7 indistinguishable. There is also considerable difference in the male postabdomens and in other characters. Whereas *Heterocheila* is restricted to cool temperate shores, eurychoromyiids are only known from Bolivia, a land-locked tropical country. I conclude that the few points of resemblance between these taxa are not indicative of close relationship.

Heterocheila is excluded from the Sciomyzidae (perhaps including Phaeomyiinae) because of the prelabrum, and its larvae feed on neither molluscs nor diplopods. Otherwise there are no special points of resemblance and no recent author has suggested a close relationship.

Heterocheila is excluded from the Huttoninidae (best regarded as a separate family, not a subfamily of Sciomyzidae or Helosciomyzidae; further discussed in the forthcoming 2nd edition of 'The Insects of Australia') because it lacks the following distinctive features of Huttoninidae: antennal segment 1 without setulae on medial surface; vein 6 abbreviated; distal section of vein 7 scarcely distinguishable; abdominal sternite 1 vestigial or absent; abdominal tergites 1 and 2 not partly separated by a membranous dorsal line. Huttoninids appear to be mainly forest-living and are endemic to New Zealand.

Heterocheila is excluded from the Helosciomyzidae because it lacks the following apparently consistent features of that family: costa with prominent spaced anteroventral spines; fronto-orbital plate with at most two bristles; prothoracic precoxal bridge absent; abdominal sternite 1 vestigial; abdominal tergite 6 of male much reduced; each posterior spiracle of larva with 4 branched hydrofuge hairs (*Helosciomyza* Hendel and *Polytocus* Lamb). Helosciomyzids are apparently restricted to the south-temperate zone. In my experience they are found in forests, grasslands, swamp-margins, and rocky shores, but are not known to inhabit kelp beds.

Heterocheila differs from the families Chamaemyiidae (including Cremifaniidae) and Lauxaniidae (including Celyphidae) in its complete vein 6 and numerous other traits. These families are morphologically more remote from *Heterocheila* than are most other sciomyzoids (J. McAlpine 1989), they are not associated with kelp, and further comparison is deemed unnecessary.

The exclusion of *Heterocheila* from all recog-

nised families of Sciomyzoidea necessitates the setting up of a new monogeneric family of this superfamily.

Heterocheilidae fam. n.

Type genus: *Heterocheila* Rondani, 1857: 104 (present designation).

Diagnostic description

Actively flying insects of maritime environments; habitus and many structural details typical of Sciomyzoidea; cuticle largely pruinose and non-shining; parts of thorax, legs, and abdomen with mollisetae, particularly developed in male.

Head. – rounded anteriorly; face somewhat convex centrally, with shallow fovea below each antenna; parafacial ridge shining, extending, together with associated suture, below cheek to postgenal region; cheek deep, setulose; postgenal fold long, distinctly incised, located towards posterior surface of head capsule; postvertical bristles often subparallel (slightly variable in orientation); fronto-orbital bristles 3, directed outwards. Antenna, at rest, subporrect; segment 1 with setulae extending on to medial surface; segment 3 rounded-oval; arista with minute pubescence, segment 5 short, not much exerted; prelabrum moderately developed, narrowly separated from face, but not fitting into sinuation on lower margin of latter.

Thorax. – Sternopleural suture not ascending posteriorly; hypopleural channel rapidly expanding anteriorly; margin of metathoracic spiracle and sternopleuron bare; prosternum broadly triangular, with narrowly sclerotised precoxal bridges; other significant characters of chaetotaxy and vestiture as in Table 1. Each tibia with one preapical dorsal bristle; all basitarsi without terminal ventral process; last 2 tarsal segments depressed and distally expanded. Costa unbroken, extending to vein 4, beyond end of subcosta with an anterodorsal series of closely placed spinules and a regular series each of dorsal, anteroventral, and ventral setulae or hairs, without spaced anterior or anteroventral spines; vein 6 visible approximately to wing margin; vein 7 beyond alula represented by long, curved crease in membrane.

Abdomen. – Tergites 1 and 2 incompletely separated by a dorsal transverse membranous line; sternite 1 short, but rather well sclerotised, bare; 7 pairs of abdominal spiracles situated in pleural membrane. Male postabdomen: tergite 6 shorter than preceding tergites but not greatly reduced, almost symmetrical, setulose; sternites 6 and 7 placed on left side; tergites 7 and 8 absent or not definitely identifiable ('8T' of Steyskal is the sclerite generally understood to be the inverted sternite 8); surstylus articulated basally, with basal anterior expansion or secondary lobe; cerci separate; basiphallus with broadly expanded membranous posterior lobe; distiphallus with complex sclerotisation and no pubescence. Female postabdomen only moderately extensive, with all segments short; tergites and sternites 6-8, epiproct, and hypoproct all well sclerotised and setulose; cerci separate, elongate.

rite generally understood to be the inverted sternite 8); surstylus articulated basally, with basal anterior expansion or secondary lobe; cerci separate; basiphallus with broadly expanded membranous posterior lobe; distiphallus with complex sclerotisation and no pubescence. Female postabdomen only moderately extensive, with all segments short; tergites and sternites 6-8, epiproct, and hypoproct all well sclerotised and setulose; cerci separate, elongate.

Nomenclatural notes

I have examined the holotype of *Heteromyza orientalis* Macquart, 1843, in the National Museum of Natural History, Paris, and find it to be identical with *Heterocheila buccata* (Fallén, 1820) (syn. n.). The given type locality of Macquart's species, Java, is erroneous; the species is probably restricted to Europe, where it is apparently absent from warmer, southern areas.

I propose the common names half-bridge flies, for representatives of the family Heterocheilidae, and bridge flies for representatives of the family Helcomyzidae. These names refer to the development of the prothoracic precoxal bridge.

ACKNOWLEDGEMENTS

I am indebted to M. C. D. Speight for help in finding *Heterocheila* in the field, to L. Tsacas and M. Baylac for the opportunity to examine type material in the National Museum of Natural History, Paris, and to W. N. Mathis and J. R. Vockeroth for study material.

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BOOK REVIEW

Knight, W. J. & J. D. Holloway (Eds), 1990. Insects and the rain forests of South East Asia (Wallacea). - The Entomological Society of London, London: p. i-iv + 1-343, figs. [ISBN 0 90546 76 3. Price £ 33.50 (incl. p & p)].

This publication is one of the results of 'Project Wallace' and includes the papers presented at a special symposium to highlight some of the major research topics undertaken during that expedition. Readers of the *Tijdschrift voor Entomologie* certainly have heard about this one year-long expedition to North Sulawesi (1985), since various results have been published in earlier volumes of this journal.

As one of the participants myself, I am still impressed by the efforts the Royal Entomological Society of London (RESL) has made for the benefit of entomology, commemorating the society's 150th anniversary. Anybody who has any experience in getting things organized for his own trips, or perhaps for smaller expeditions, in tropical countries, knows about the difficulties. Logistics under primitive conditions and co-ordination of enforced co-operation between scientists were some of the organizational pitfalls the leaders of this expedition had to observe. Also the Indonesian government should be congratulated with usually adequate handling their problems. Dozens of servicemen and scientists, flying in and out via Jakarta, all had to get their correct 'surat' (letters) on time. Especially the bureau of Lembaga Ilmu Pengetahuan Indonesia, co-ordinating all the foreign scientific activities in Indonesia, must have heaved a sigh of release on December 31st, 1985.

From a biogeographical point of view, Sulawesi is one of the most interesting places on earth, as was already noticed by Alfred Russel Wallace. The geology of Sulawesi is extremely complex. The expedition was held in the Dumoga-Bone National Park, which is approximately central in the Minahasa peninsula. This peninsula is considered to be a part of an island of Oriental derivation. The central-eastern and south-eastern peninsula together formed once another island, probably of Australasian origin. Both islands collided only in the Miocene, and the latter island emerged above sea level only since that time. The National Park is fully covered with rain forest, and the protection of the forest is of high importance for the safeguarding of the water catchment of the Dumoga Plain, which is now a transmigration area.

Although the present volume has to be considered as the final report of the expedition, it is apparent from most papers that the study of the

material has only just begun. The insect fauna of Sulawesi was nearly completely unknown, except for some groups attracting also the general collector. With so many specialists collecting their own groups, and the extensive general sampling programs with malaise traps, light traps and fogging, literally millions of specimens have found their way to museums. It will take long until all the specimens are named. Just a few examples. In the Ephemeroptera not one species was reported from the whole of Sulawesi; now Edmunds and Polhemus mention the existence of twenty genera with one to four undescribed species per genus. Preliminary sorting of the beetles collected by the British Museum (Natural History) revealed an estimated total of more than 5500 species.

For the general reader interested in biodiversity and ecology, Hammond's report on the BMNH's study program, including large scale malaise trapping and fogging (a method to sample the canopy fauna using insecticides), is highly relevant, both for the description of the methods as well as for the results. For instance, it is claimed now that the percentage of plant-associated beetles in tropical ecosystems may prove to be far less than an estimation based on described species alone would suggest. In the present studies, no less than 29% of the beetles collected were predators and only 17% herbivores. Hammond also concludes that all but 18 of the 130 beetle family-groups collected in northern Sulawesi were found at light. For 49 beetle groups light trapping produced even a greater number of species than any other method.

For biogeographers there is also a lot of new information. Although the fauna of Sulawesi seems to be Oriental rather than Australian, a direct faunal exchange between Sulawesi and Borneo seems to have occurred very rarely. Vane-Wright presents good evidence that the relationship between the fauna of the Philippines and Sulawesi is stronger than generally accepted. Also, it seems that Sulawesi has been an important source for the Moluccas plus New Guinea. A sister relation between Sulawesi and eastern Indonesia has been confirmed in several taxonomically unrelated groups (e. g. the danaid genus *Idea*, Cicadidae). Of course, Sulawesi is particularly of interest for its huge percentage of endemics, as can be expected for an isolated area that increased considerably in size after a long period of relative stability. Apart from the taxonomic groups mentioned before, there are also contributions on Hesperidae, rodent ectoparasites, aquatic Heteroptera, Phoridae, Tetrigidae and catantopine Acrididae. Furthermore, there are papers on the physiography and vegetation of the

Continuation on p. 278

TAXONOMY AND DISTRIBUTION OF THE *TRIFURCULA* (*GLAUCOLEPIS*) *RAIKHONAE* GROUP (LEPIDOPTERA: NEPTICULIDAE)

Nieukerken, E. J. van & R. Puplis, 1991. Taxonomy and distribution of the *Trifurcula* (*Glaucolepis*) *raikhonae* group (Lepidoptera: Nepticulidae). – Tijdschrift voor Entomologie, 134: 201-210, figs. 1-22. [ISSN 0040-7496]. Published 18 December 1991.

Trifurcula (*Glaucolepis*) *melanoptera* sp. n. is described from southern Europe, where it is widespread. It is closely related to the Central Asian *T. (Glaucolepis) raikhonae* Puplis, which is redescribed. Together they form the *raikhonae* species group. *Sinopiticula* Yang is here synonymized with *Glaucolepis* Braun, its only species *S. sinica* Yang is tentatively regarded as closely related, if not conspecific with *T. raikhonae*. The distribution is mapped. On the basis of recent Chinese findings the larvae are assumed to be gall-makers on *Prunus* branches. Some phylogenetic and biogeographic remarks are given.

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Key-words. – Microlepidoptera, Central Asia, Southern Europe, biogeography, phylogeny, gall-former, new species.

The subgenus *Glaucolepis* Braun, 1917, is one of three subgenera of *Trifurcula* Zeller, 1848 (van Nieukerken 1986b, 1990). It comprises to date 21 described species (see van Nieukerken 1986a, 1986b) and a large number of undescribed species. Most of these occur in the Mediterranean region. The type species *T. saccharella* (Braun, 1912) is the only Nearctic species. Further, one undescribed species occurs in Japan, one in North-East India and *T. raikhonae* (Puplis, 1985) in Central Asia. In treating *Glaucolepis* as a subgenus, we follow the opinion of the senior author, whereas the junior author prefers to treat it as separate genus (Puplis 1985).

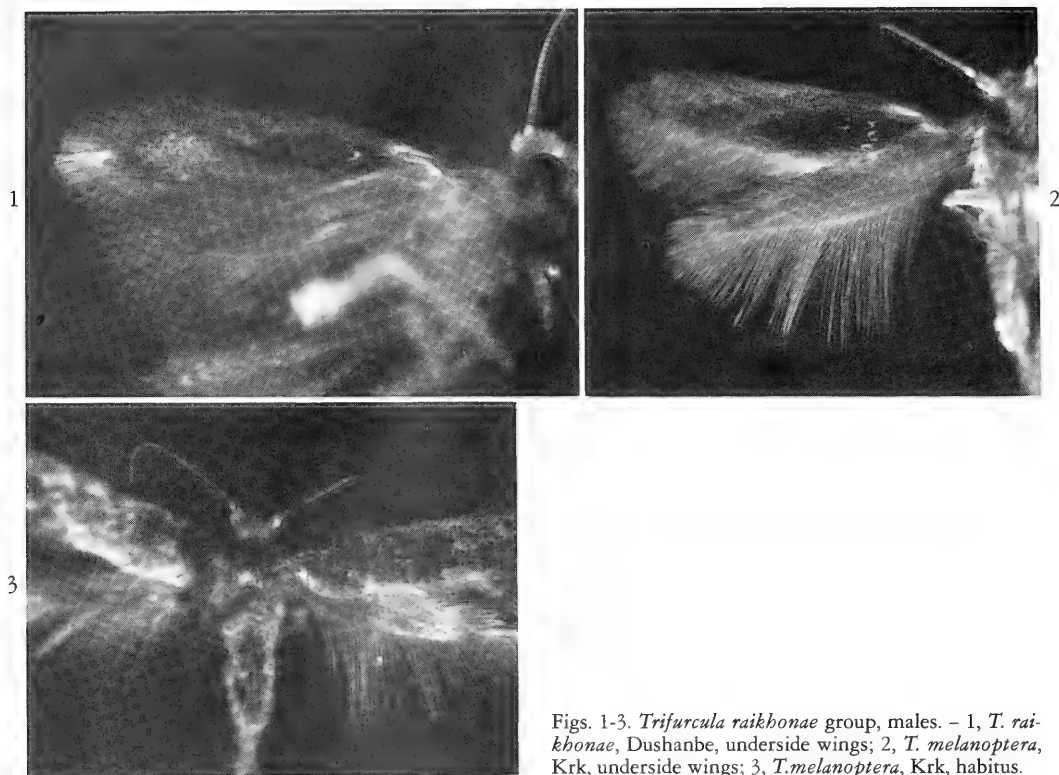
Amongst unidentified material from southern Europe, one apparently widespread species very similar to *T. raikhonae* was found by both authors independently. Although a revision of the many mediterranean species is not yet practicable at this stage, we would like to single out this peculiar species, because it forms a well defined monophyletic group with *T. raikhonae*: the *raikhonae* species group. This group can easily be distinguished from all other species in the subgenus, both on externals and genitalia and possibly also on biology. It was also desirable to have the new name

available for a general work on Nepticulidae of the Soviet-Union and other faunistical reports. We further take the opportunity to redescribe *T. raikhonae* for the first time in English, including new data and the description of the female, and to discuss a recently described Chinese taxon. Some remarks on phylogeny and biogeography conclude this paper.

MATERIAL AND METHODS

Genitalia were prepared as described by van Nieukerken et al. (1990). Line figures of genitalia were prepared with a Zeiss Axioskop with drawing apparatus, both from genitalia in glycerin and permanent mounts. SEM micrographs were taken with a Jeol JSM 840A scanning electron microscope. Specimens were air-dried, mounted on stubs and gold-coated.

Measurements of genitalia are taken with a Zeiss Axioskop at 200X, and are accurate at the nearest 5 µm. Capsule length is measured along mid-line, from tip of tegumen (pseuduncus) to anterior margin of vinculum, in middle. All measurements based on sample size of at least five specimens are accompanied by mean, standard deviation and sample size in brackets.



Figs. 1-3. *Trifurcula raikhonae* group, males. - 1, *T. raikhonae*, Dushanbe, underside wings; 2, *T. melanopectera*, Krk, underside wings; 3, *T. melanopectera*, Krk, habitus.

Locality names are spelled in accordance with the Times Atlas of the World (Comprehensive edition 1975 and later). For all European localities the appropriate UTM grid references are given, see also van Nieukerken (1990).

Abbreviations (codens) for depositories follow Arnett & Samuelson (1986), with the addition of ZKVV (Zoologijos Katedra VPI, Vilnius, Lithuania).

SYSTEMATIC PART

Subgenus *Glaucolepis* Braun

Glaucolepis Braun, 1917.

Fedalmia Beirne, 1945.

Trifurcula (*Glaucolepis*); van Nieukerken 1986b: 65.

Sinopticala Yang, 1989: 79, 81. Type-species: *Sinopticala sinica* Yang, 1989 (by monotypy and original designation). Syn. n.

Recently, Yang (1989) described *Sinopticala sinica* from China. Although we have been unable to borrow material, we are convinced on the basis of description and figures that this species is closely related to, if not the same as *T. raikhonae*. We therefore synonymize *Sinopticala* here with *Glaucolepis*, and hence with *Trifurcula*.

For description of genus and subgenus and detailed references we refer to van Nieukerken (1986b).

The *Trifurcula raikhonae* group

This group is established here to accommodate *T. raikhonae*, *T. sinica* and *T. melanopectera* sp. n. It can be distinguished from other species of *Trifurcula* (*Glaucolepis*) by the absence of the 'velvet' patch of raised scales on the male hindwing underside, the presence of dark brown or black androconial scales on the forewing underside, the absence of rows of spines near phallotreme in the aedeagus and the relatively well developed accessory sac in the female genitalia.

Trifurcula (*Glaucolepis*) *raikhonae* (Puplesis) (figs. 1, 3, 5-7, 14, 17-19)

Glaucolepis raikhonae Puplesis, 1985: 71. Holotype ♂: USSR, Tadzhikistan, about 30 km S Dushanbe, Kondara canyon, 10-20 June 1982, Sherniyazova (ZMAS) [examined].

Trifurcula raikhonae; van Nieukerken 1986b: 68.



Fig. 4. Distribution of *Trifurcula raikhonae* group in east Palearctic. —Circles: *T. raikhonae*, square: *T. sinica* (Xi'an), triangle: easternmost record of *T. melanoptera* (Kopet Dag).

Description

Male (fig. 1). — Forewing length 3.1–3.9 mm (3.42 ± 0.19 , $n=32$). Head: frontal tuft pale orange to ferruginous, collar slightly paler. Antenna brown, with 45–56 segments (50.3 ± 3.0 , $n=19$); scape yellowish white. Thorax fuscous. Forewings fuscous, slightly irrorate with white because of paler scale bases; dorsum often paler, with some white scales at tornus, sometimes extending further; cilia-line more or less distinct, terminal cilia pale grey. Forewing underside anterior of fold usually with an elongate patch of about $\frac{1}{2}$ wing-length and $\frac{1}{2}$ wing-width, with dark fuscous to black androconial scales (fig. 1), usually with blue iridescence, occasionally patch absent or paler and almost invisible. Hindwing grey, humeral lobe with a small group of extremely small whitish special scales, macroscopically hardly visible, distinct under SEM (figs. 17–19): they are strongly ribbed, with small holes between the ribs; in fig. 19 it seems that the scale has an apical pore. Costal bristles normal; underside without velvet patch as most other *Trifurcula* (see van Nieukerken 1986b, 1990). Abdomen grey-brown dorsally, yellowish ventrally; three pairs of anal tufts yellowish grey.

Female. — Forewing length 3.2–4.0 mm (3.56 ± 0.26 , $n=8$). Antenna with 42–49 segments (44.8 ± 2.6 , $n=5$). Forewing underside grey-brown, further as male.

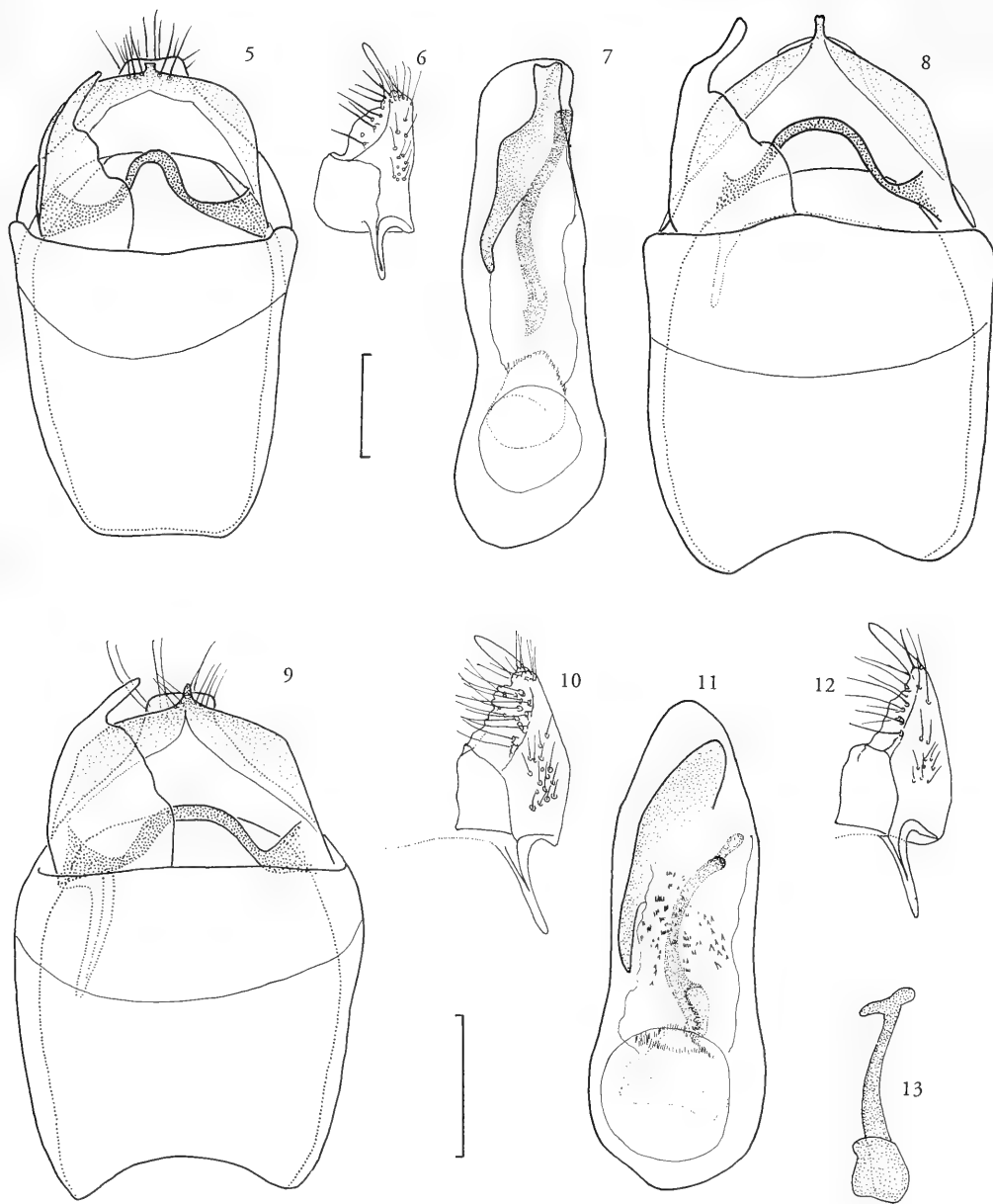
Male genitalia (figs. 5–7). — Capsule length 390–470 μm (430.0 ± 27.7 , $n=6$). Vinculum with very long, truncate, anterior extension, length (190) 245–280 μm , ca (0.5) 0.6 \times capsule length. Tegumen

men forming a broadly truncate pseuduncus. Uncus with slightly widened tip, truncate, lateral arms broadly shouldered, very conspicuous. Gnathos with broadly rounded central element, lateral arms inserted on vinculum near valva base. Valva short, 165–185 μm long, almost triangular, with pointed narrow tip of about $\frac{1}{3}$ valva length, inner margin with slight bulges in second half; sublateral process relatively short, transverse bar of transtilla not sclerotized, but present. Aedeagus 365–430 μm (400.0 ± 22.4 , $n=6$) long, with asymmetrical ventral lobe, more sclerotized at left side; single long cornutus 185–235 μm long, about $\frac{1}{2}$ aedeagus length, slightly curved, tip more or less rounded; cathrema large, almost triangular, no additional cornuti.

Female genitalia (fig. 14). — Terminal segments blunt and rounded; T8 with groups of many scales and several setae, anal papillae with 34–53 setae each. Vestibulum with conspicuous folded accessory sac. Ductus spermathecae outer canal wide and distinct, inner canal strongly sclerotized, with long basal straight part, followed by 7 convolutions. Bursa relatively small, covered with transverse rows of pectinations and single spicules; reticulate signa very inconspicuous, only visible under high magnification, using phase-contrast or differential interference contrast; cells mostly incomplete, recognized by longitudinal groups of pectinations.

Diagnosis

From other species of *Glaucolepis*, *raikhonae* differs by the absence of a velvet patch on the male



Figs. 5-13. *Trifurcula raikhonae* group, male genitalia – 5-7, *T. raikhonae*, Tadzhikistan, slide EJvN 2787; 8-13, *T. melanoptera*: 9-11, holotype, slide EJvN 2786; 8, 12, Turkey, slide EJvN 2784; 13, Armeniya, slide RP. – 5, 8, 9, capsule, ventral aspect; 6, 10, 12, left valva, dorsal aspect; 7, 11, aedeagus, ventral aspect; 13, cornutus, ventral aspect, but slightly rotated compared to fig. 11. Scales: 0.1. mm, top to *raikhonae*, bottom to *melanoptera*.

hindwing underside, the relatively large size and the frequently present androconial patch on forewing underside. It is currently the only known Central Asiatic *Glaucolepis*, and can therefore hardly be confused with any other nepticulid of the area. It differs from the only other Central Asiatic *Trifurcula* species, *T. puplesisi* van Nieukerken, 1990, by its larger size, dark colour and in male by absence of yellow patch on forewing underside and velvet patch on hindwing. For differences with *melanopectera* see below.

Biology

Unknown, but considering the biology of the closely related, if not conspecific *sinica*, possibly also a gall-maker of *Prunus*. Various *Prunus* species are widespread and common in the Central Asian mountains. Adults found from May to August, at light.

Distribution (fig. 4)

Widespread in Central Asian mountains: western and central Tyan Shan (Kazakhstan and Kirgiziya), Gissarskiy (Hissar) ridge (Tadzhikistan), and northern Kugitangtau mountains (Uzbekistan) and in central Afghanistan. Previously only known from two specimens in Tadzhikistan and Kirgiziya (Puplesis 1985). Not found in lowland desert areas.

Material examined. – Afghanistan: 1 ♂, Paghman, 30 km NW Kabul, 2100 m, 20.30.vii.1962, E. & A. Vartian (NHMW); 1 ♂, same locality, 2500 m, 15.18.vii.1965, Kasy & Vartian (NHMW). – USSR: Kazakhstan: 11 ♂, 1 ♀, Tyan Shan, 90 km E Chimkent, 1300 m, Aksu Dzhabagly, 7.12.viii.1987, Sheriyazova (ZKVV, RMNH) – Kirgiziya: 1 ♂ (paratype), 5 km SW Naryn, 26.vii.1981, Sinev (ZMAS); 2 ♂, 2 ♀, Sosnovka, 40 km S Kara Balty, 13.viii.1987, Lvovskiy (ZMAS). – Uzbekistan: 3 ♂, env. Derbent, 18.v.1985, R. Puplesis (ZKVV, RMNH). – Tadzhikistan: ca 90 ♂, ♀, 30 km N Dushanbe, Kondara, 27.vi–20.viii.1986, R. Puplesis (ZKVV, RMNH); 13 ♂, 6 ♀, idem, but 17–20.viii.1989 (ZKVV).

Trifurcula (Glaucolepis) sinica (Yang) comb. n.

Sinopticala sinica Yang, 1989: 80, 82. Holotype ♂: China, Shaanxi prov., Xi'an, emerged 24–30.iv.1985, from galls on *Prunus*, Yan-wen (Beijing Agricultural University) [not examined]

Remarks

The relatively detailed description of *Sinopticala sinica* Yang, 1989 and the small, but distinct figures show many similarities to *raikhonae*. The slight differences in the form of the valvae in Yang's figure from the usual shape in *raikhonae* might be

due to the preparation technique. Without detailed examination we would rather not synonymize *sinica* here, although we suspect that it indeed is conspecific with *raikhonae*. The locality Xi'an is at the east end of the almost continuous Central Asian mountain ranges, in which *raikhonae* presumably is widespread.

Biology

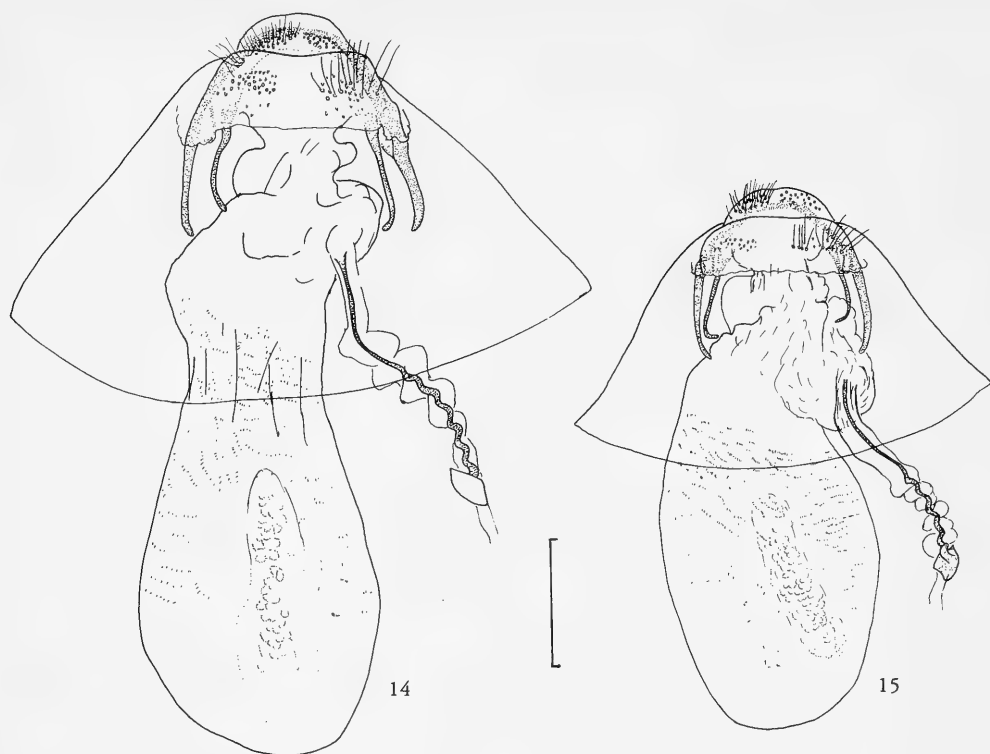
According to Yang (1989) the larvae make galls in young branches of *Prunus cerasifera* Ehrh., *P. dulcis* (Miller) D. A. Webb (= *P. amygdalus* Bartsch) and *P. persica* (L.) Batsch. It is not clear from the description, how these galls look like. Adults emerged in April.

Distribution (fig. 4)

Only known from China, Shaanxi province.

Trifurcula (Glaucolepis) melanopectera sp. n. (figs. 2, 3, 8–13, 15, 16, 20–22).

Type-material. – Holotype: ♂, Yugoslavia (Croatia), Krk, Misucaynica [UTM: 33T VK78], 4.viii.1986, G. Bal-dizzone, Genitalia slide E. J. van Nieukerken No. 2786 (RMNH). – Paratypes: 52 ♂, 3 ♀: Austria: 1 ♂, Hackels-berg, N. Neusiedlersee (N. Burgenland) [UTM: 33U NV52], 24.viii.1973, F. Kasy (NHMW). – Czechoslovakia: 3 ♂, Slovakia, Turňa n. B. [UTM: 34U DU9183], 4–5.viii.1990, A. Laštůvka (coll. Laštůvka); 1 ♂, Slovakia, Tinianska stran [NE Michalovce] [UTM: 34U EV60], 20.viii.1989, Z. Tekár. – France: 1 ♀, Les Mees (Alpes de Haute Provence) [UTM 31T GJ37], 28.viii.1985, G. Langohr (RMNH); 1 ♂, Chapeau [not traced, near Digne?], 27.vii.1903, Chrétien (MNH); 12 ♂, 1 ♀, Viens (Vau-cluse) [UTM: 31T GJ06], 9.viii.1973, 14.vii–23.viii.1974, 6.viii.1975, 9–27.viii.1976, 15.viii.1979, 8.viii.1980, 12.viii.1982, R. Buvat (RMNH, coll. Buvat). – Italy: 1 ♂, Sardinia, Bacu Trotu, Ortuabis 800 m [UTM: 32S NK11], 23.viii.1978, Gg. Derra (coll. Derra). – Spain: 1 ♂, Cadalso (Madrid) [UTM: 30T UK86], 15.vii.1985, C. Gielis (coll. Gielis); 2 ♂, Cadalso de los Vidrios, 2 km E (Madrid), [UTM: 30T] UK8062, 7.viii.1986, at light ML, matorral, cult. area, E. J. van Nieukerken & S. Richter (RMNH); 1 ♂, Noguera (Teruel), [UTM: 30T XK17], 9–10.viii.1989, C. Gielis (coll. Gielis); 1 ♂, Paterna del Madera (Albacete), 1350 m [UTM: 30S WH57], 18.vii.1986, C. Gielis (RMNH); 1 ♀, Pto de Mora (Granada) 1350 m [UTM: 30S VG52] 22.vii.1986, C. Gielis (RMNH); 1 ♂, Riazza (Segovia), [UTM: 30T VL57], 3.viii.1986, C. Gielis (coll. Gielis); 1 ♂, San Miguel de Valero (Salamanca), 3 km S Linares de Riofrio, [UTM: 30T] TK59, 2.viii.1986, at light ML, *Quercus pyrenaica* forest and heathland, 850 m, E. J. van Nieukerken & S. Richter (RMNH); 2 ♂, Vega del Codorno (Cuenca), 1350 m, [UTM: 30T WK97], 23.vii.1985, at light, J. H. Kuchlein (RMNH, coll. Kuchlein). – USSR, Turkmeniya: 1 ♂, 30 km E Kara Kala, (Western Kopet Dag range), env. Juvankala [UTM: 40S DH35], 18.viii.1988, R. Puplesis (RMNH) – USSR, Ukraina: 2 ♂, Crimea, Kara Dag, 20 km W Feodosia [UTM: 36T XQ78],



Figs. 14, 15. Female genitalia, dorsal aspect. – 14, *T. raikhonae*, Tadzhikistan, slide EJV N 3205; 15, *T. melanopectera*, paratype, Spain, slide EJV N 3102. Scale: 0.2 mm.

3.viii.1986, Buhashkim (ZMAS); 1 ♂, same data, 13.vii.1987, Sinev (ZMAS); 6 ♂, same data, 15-22.vii.1987, R. Puplesis (ZKVV, RMNH). – Yugoslavia (Croatia): 1 ♂, Krk, no further data, 10.viii.1975, at light, G. Baldizzone (Coll. Baldizzone); 2 ♂, 1 ♀, Krk, Draga Baska [UTM: 33T VK78], 30.vii.1986, 15.viii.1988, G. Baldizzone (RMNH, coll. Baldizzone); 2 ♂, Krk, Misucaynica [UTM: 33T VK78], 19.viii.1986, G. Baldizzone (coll. Baldizzone); 10 ♂, Krk, road Krk-Vrbnik [UTM: 33T VK78], 2, 18.viii.1987, 20.vii-11.viii.1988, G. Baldizzone (RMNH, ZKVV, coll. Baldizzone).

Material excluded from type series (34 ♂). – Hungary: 30 ♂ (all in poor condition), Budapest, Julianna Major, apple orchard, 9+11.viii.1991, glued pheromone traps, M. Tóth (RMNH). – Italy: 1 ♂, Latina, Monti Aurunci, 850 m, 5 km N Itri [UTM: 33T UF77], 4-11.viii.1972, R. Johansson (coll. Johansson). – Turkey: 2 ♂, 10 km NW Kizilcahan (Ankara), 1150-1250 m [UTM: 36T VK68], 6-7.viii.1989, Fibiger & Esser (ZMUC). – USSR, Armenia: 1 ♂, Chosrov reserve [UTM: 38S MK82], 20.ix.1986, P. Ivinskis (ZKVV).

Description

Male (figs. 2, 3). – Forewing length 2.4-3.0 mm (2.74 ± 0.12 , 29), wingspan 5.8-6.9 mm. Head: frontal tuft pale orange to ferruginous, collar

slightly paler. Antenna brown, with 40-45 (42.2 ± 1.4 , 23) segments; scape yellowish white. Thorax fuscous, often distally paler. Forewings fuscous, slightly irrorate with white because of paler scale bases; dorsum with narrow stripe of white scales, occasionally reduced to white tornal spot; cilia-line more or less distinct, terminal cilia pale grey. Forewing underside anterior of fold almost completely covered with dark fuscous to black androconial scales, usually with blue iridescence, except at wing tip, which is greyish-brown. Ultrastructurally with many circular holes between ribs (figs. 21, 22). Hindwing grey, humeral lobe with few fuscous androconial scales, as forewing; occasionally these scales extending on hindwing upperside along Rs+M, forming an elongate patch; costal bristles forming a short brown hair-pencil; near frenulum a group of microtrichia, no scales (fig. 20); underside without velvet patch as most other *Trifurcula*. Abdomen grey-brown dorsally, yellowish ventrally; three pairs of anal tufts yellowish grey.

Female. – Forewing length 2.75-3.0 mm, wingspan 6.4-6.7 mm. Antenna with ± 39 segments. Forewing underside dark grey-brown, darker than

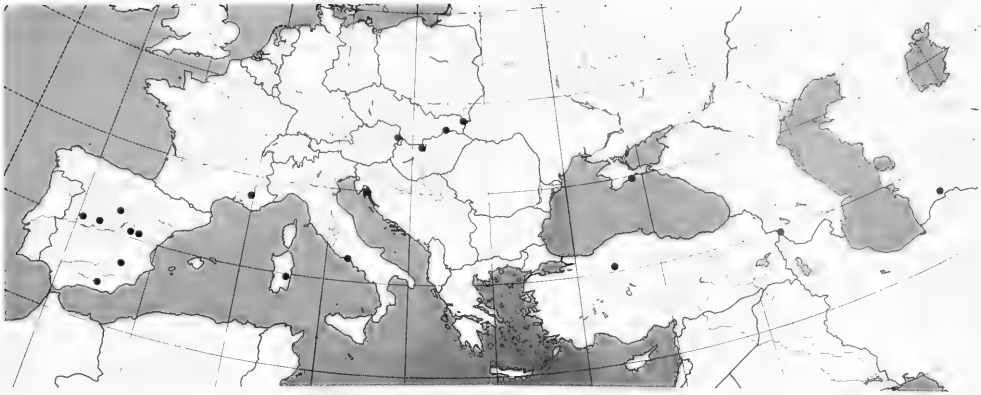


Fig. 16. Distribution of *Trifurcula melanoptera*, mapped on 50 km squares of UTM grid.

hindwing. Otherwise as male. Ovipositor wide and truncate.

Male genitalia (figs. 8-13). – Capsule length 305-390 μm (345 ± 20.3 , $n=11$). Vinculum with very long, truncate, anterior extension, length 200-260 μm , ca 0.6-0.7 \times capsule length. Tegumen forming a broadly truncate pseuduncus. Uncus with slightly widened tip, or pointed, lateral arms shouldered, but less than in *raikhonae*. Gnathos with broadly rounded central element, lateral arms inserted on vinculum near valva base. Valva short, 140-165 μm (149.1 ± 6.3 , $n=11$) long, almost triangular, with pointed narrow tip of about $\frac{1}{3}$ to $\frac{1}{4}$ valva length, inner margin with slight bulges in second half; sublateral process relatively short, transverse bar of transtilla not sclerotized. Aedeagus 325-390 μm (356.8 ± 18.4 , $n=11$) long, with distinct asymmetrical ventral lobe, sclerotized at left side, with anterior point; single long cornutus 130-205 μm long, slightly less than $\frac{1}{2}$ aedeagus length, curved, tip distinctly bifurcate, with rounded lobes forming an angle of almost 180° (fig. 13); several additional small cornuti, some forming 'pectinations'; caethrema large, almost triangular.

Female genitalia (fig. 15). – Very similar to those of *T. raikhonae*, but smaller. Anal papillae with 25-30 setae each. Accessory sac of bursa even larger than in *raikhonae*. Ductus spermathecae with $5\frac{1}{2}$ to $6\frac{1}{2}$ convolutions.

Diagnosis

Very similar to *T. raikhonae*, but distinctly smaller and in male with much larger androconial patch on forewing underside and with small similar patch on humeral lobe of hindwing. In male genitalia easily distinguished by the bifurcate cor-

nutus. In female genitalia by larger accessory sac and smaller bursa. From other southern European species of *Trifurcula*, males of *melanoptera* differ by the absence of a velvet patch on the male hindwing underside, and the large black or fuscous androconial patch on the forewing underside.

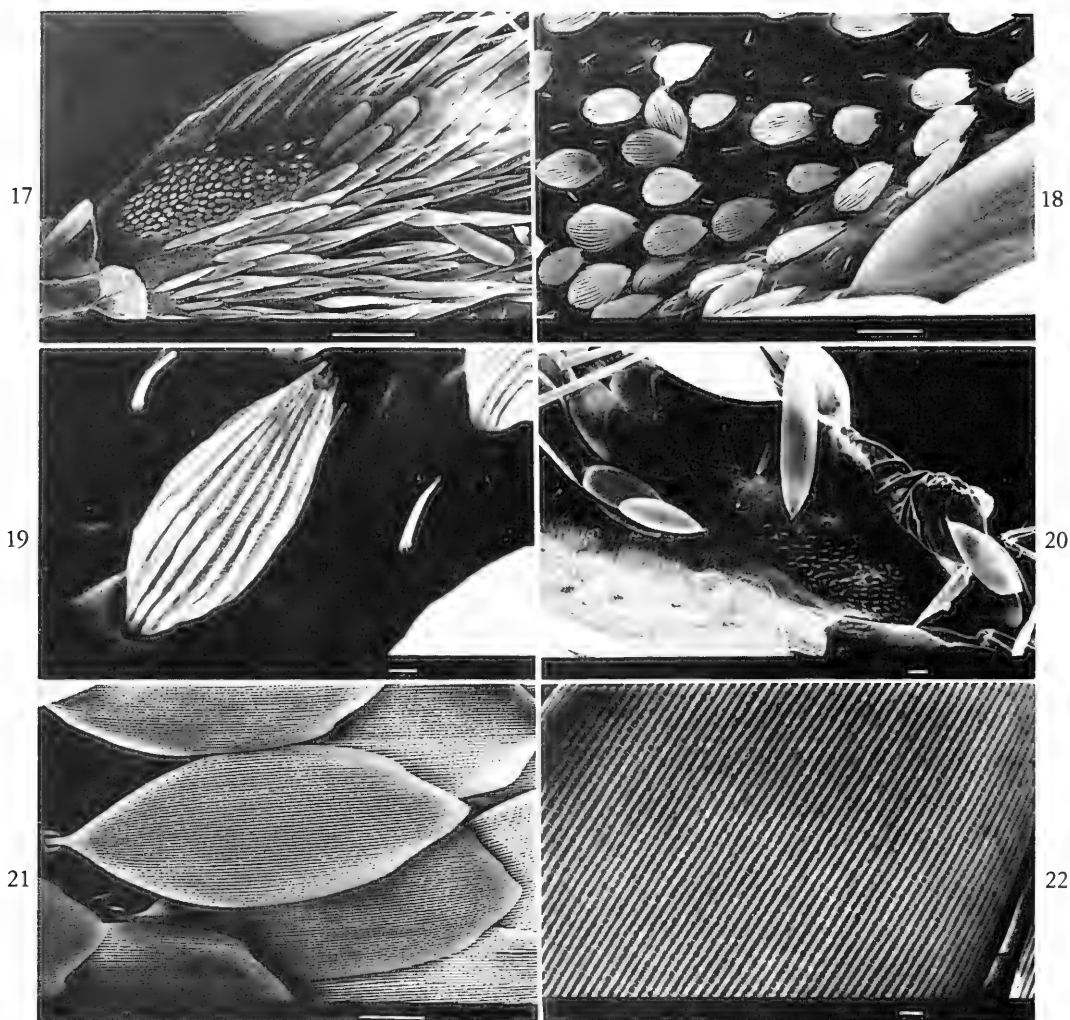
Variability

Specimens from Turkey and Armenia differ from the remaining material by the presence of androconial scales on the hindwing upperside. Also the genitalia of especially the Armenian specimen differ slightly in size, shape and position of cornutus. However, these characters seem to vary within the whole distribution area, with the Armenian specimen as the extreme example. Since we also observed few androconial scales on the hindwings of some other specimens, we tentatively assume that *melanoptera* forms one widespread, slightly variable species, until more data become available.

It should also be noted that the specimen from Italy, Itri, has relatively small genitalia, which look slightly different, but tentatively is regarded as an aberration. Both this specimen and the Turkish and Armenian specimens are excluded from the type series.

Biology

Immature stages and hostplant unknown. Judging from its close relationships with *T. raikhonae* (and hence *sinica*), it is not impossible that also *melanoptera* is a gall-maker on *Prunus*. In some localities, visited by the senior author, such as Viens, France, *Prunus spinosa* L. was abundant; galls were, however, not yet seen. The record of



Figs. 17-22. *Trifurcula raikhonae* group, male scale structures, scanning micrographs. – 17-19, *T. raikhonae*, hindwing humeral lobe, upperside: patch of small special scales, with details. 20-22, *T. melanoptera*: 20, hindwing humeral lobe with group of microtrichia and special scales (left); 21, 22, androconial scales of forewing underside with many circular holes. Scale bars: 100 μ m (17), 10 μ m (18, 20, 21), 1 μ m (19, 22).

males taken in pheromone traps in an apple orchard in Budapest does not contradict this, since this orchard contains several fruit trees, including *Prunus* spp., and is surrounded by shrub with much *Prunus spinosa* (G. Szöcs in litt.).

Adults caught from 13 July to 28 August, in Armenia on 20 September, most likely univoltine.

Distribution (fig. 16)

Widespread in southern Europe: Spain, south-

ern France, Italy, Sardinia, Austria, Czechoslovakia, Hungary, Yugoslavia and Crimea and in western Asia: Anatolia, Armenia and western Turkmeniya (Kopet-Dag range).

Etymology

A noun in apposition. From *melanos* (Greek), black and *ptera* (Greek), wings, referring to the black androconial scales on the forewing underside in the males.

PHYLOGENETIC AND BIOGEOGRAPHIC CONSIDERATIONS

The two species discussed here clearly belong to *Trifurcula* Zeller s. l., since they possess four out of the six apomorphies for this taxon as listed by van Nieukerken (1986b: 63). Character 44 (velvet patch of raised androconial scales on male hind-wing-underside) is absent in both species, as is also the case in *Trifurcula* (*Glaucolepis*) *saccharella* (Braun, 1912), the type species of *Glaucolepis*. Since this patch is present in all other *Trifurcula* species, examined by us, it has most likely been secondarily lost in these three species. The doubtful apomorphy 45 (Hostplant: Fabaceae) has already been discussed by van Nieukerken (1986b).

The *T. raikhonae* species group is here regarded as belonging to *Glaucolepis*, with which it shows the closest similarity. Van Nieukerken (l.c.) only lists three apomorphies for *Glaucolepis*: the species under discussion show some deviations in these characters:

48. Transverse bar of transtilla lost. In both species the transverse bar is apparent, although it is not present as a sclerotized bar. We tentatively assume that this can be regarded as a first step towards the complete loss of the transverse bar.

49. Aedeagus with spines near phallotreme: these are completely lacking in the *raikhonae* group.

50. Vesica with single long cornutus: the vesica here has indeed one long cornutus, but unlike other *Glaucolepis* species studied, in *T. melanoptera* there are some additional small cornuti present.

We believe that the condition of character 48 and 50 in the *raikhonae* group and the large similarity of the male genitalia in general are sufficient for inclusion in *Glaucolepis*. On this basis we also have synonymized *Sinoptricula* Yang. However, it is not unlikely that this group belongs to a clade, which is the sistergroup to all remaining known species of *Glaucolepis*. Character 49 could then be an apomorphy for the remaining species.

An additional apomorphy for *Glaucolepis*, including the species under study, is possibly the long, straight basal part of the ductus spermathecae, proximal to the coiled part. In *Trifurcula* s. str. and in *Levarchama* Beirne, the coiled part starts almost immediately near the vestibulum.

The close similarity in many characters between *T. raikhonae* and *melanoptera* makes it very likely that both share a common ancestor, which once was widely distributed in the Palaearctic. The species now have a completely vicariant distribution: *melanoptera* has a distribution type which very much resembles those of holomediterranean ele-

ments of the expansive type (De Lattin 1967), whereas *T. raikhonae* is widespread in the Central Asian mountains. Although *melanoptera* occurs as far east as the Kopet-Dag mountains in Turkmeniya, the deserts between this range and the Central Asian mountains (southern parts of the Karakum) form an important gap, which is apparent in the distributions of many taxa (Kryzhanovskij 1965, De Lattin 1967, Matyushkin 1982). Although the present-day desert could be an important barrier, the separation most likely goes back to the Pleistocene, when Europe and Central Asia were separated by the enlarged Aralo caspian Sea and the West Siberian Ice lake, or extensions of the continental ice-shields (De Lattin 1967, see also review in Tangelder 1988).

ACKNOWLEDGEMENTS

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Nieukerken, E. J. van, 1990. The *Trifurcula subnitidella* group (Lepidoptera: Nepticulidae): taxonomy, distribution and biology. – *Tijdschrift voor Entomologie* 133: 205-238.

Unfortunately the following errors have been overlooked during proof-reading of the above cited paper:

p. 207. – Figs. 7-10: figs 9 and 10 have been accidentally interchanged, the left figure with no. 9 actually is fig. 10 (*T. coronillae*), the right one is fig. 9 (*T. subnitidella*). Arrows in figs 8-10 have been omitted.

p. 222. – Figs. 57-60. Abbreviations: bs=black scales; cf=costal fold; fw=forewing; hw=hindwing; yp=yellow patch.

p. 228. – The sentences after the last paragraph of p. 228 (male genitalia of *iberica*) were accidentally omitted during page formatting:

[sublat-]eral processes. Aedeagus 335-340 μm long, with ventral carina fringed; aedeagal tube posteriorly spatulate, dorsal lobe at right side conspicuous, with serrate margin; vesica with one long spine-like cornutus (125-145 μm), with blunt tip, joined basally to a conical cornutus (50 μm); further a large cornutus with serrate tip; very few long spine-like cornuti and numerous small ones. Juxta fig. 78.

p. 230. – Line 1-2, right column: read hind-wing instead of hindwing.

In some holotype designations, the genitalia slide number has not been mentioned, they are:

- p. 219, 5. *T. victoris*: Genitalia slide EvN 2743.
p. 225, 7. *T. josefklimeschi*: Genitalia slide EvN 2744.
p. 228, 8. *T. iberica*: Genitalia slide EvN 1928.
p. 230, 9. *T. silviae*: Genitalia slide EvN 2742.

PHYLOGENY OF THE TIPULOIDEA BASED ON CHARACTERS OF LARVAE AND PUPAE (DIPTERA, NEMATOCERA)

with an index to the literature except Tipulidae

Oosterbroek, P. & Br. Theowald, 1991. Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera), with an index to the literature except Tipulidae. – *Tijdschrift voor Entomologie* 134: 211-267, figs. 1-180. [ISSN 0040-7496]. Published 18 December 1991.

Phylogenetic relationships of the Tipuloidea (the families Limoniidae, Cylindrotomidae and Tipulidae) are discussed on the basis of larval and pupal characters. In comparing outgroups, special attention is given to the synapomorphies listed by Wood & Borkent (1989) for the infraorder Psychodomorpha. In total 105 characters of larvae and pupae are evaluated. A phylogeny is presented for the Tipuloidea as well as for the genera of the subfamilies Eriopterinae, Hexatomiinae, Pediciinae and Limoniinae. An index to the literature on the immature stages except Tipulidae is added.

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Keywords. – Phylogeny, Tipuloidea, Psychodomorpha, Nematocera, larvae, pupae.

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1. INTRODUCTION

The primary concern of this paper are the characters of larvae and pupae of Tipuloidea and their contribution to our understanding of phylogenetic relationships among and within the major groups. Translation of the available information into a formal classification is considered premature for several reasons. Characters of the adults are not yet evaluated phylogenetically. Moreover, immature

stages are known for representative species of about 150 genera and subgenera, mainly from the Northern Hemisphere, which is about one-third of the recognized genera and subgenera worldwide. Progress in our knowledge of the immature stages of Southern Hemisphere taxa is very important and might well influence certain aspects of the postulated relationships.

Tipuloidea as discussed in this paper is identical to: (a) the superfamily Tipuloidea sensu Hennig (1973), comprising the families Limoniidae, Cylindrotomidae and Tipulidae, (b) the family Tipulidae s.l. of most North American and British workers, who usually recognize one family with three subfamilies, (c) the infraorder Tipulomorpha sensu Wood & Borkent (1989).

The family Limoniidae is, with about 10,000 described species, one of the largest families of Diptera. Five subfamilies are usually recognized. Immature stages of one subfamily, the Lechriinae (three genera with a limited number of species in Africa, SE Asia and Australia) are not known. The other four subfamilies, Eriopterinae, Hexatomiinae, Pediciinae and Limoniinae, are discussed

below. The tribal arrangement of the Palaearctic genera of Limoniidae is given by Dienske (1987), Savchenko (1989) and Savchenko et al. (1992).

In Cylindrotomidae about 70 species have been described, in two subfamilies, Cylindrotominae and Stibadocerinae. Information about the immature stages of the latter subfamily (four small genera in SE Asia and Chile) is not available.

The family Tipulidae accounts for some 4100 described species. Holarctic genera are assigned by some workers to three subfamilies, Dolichozeinae, Ctenophorinae and Tipulinae. This subdivision is not corroborated by the phylogenetic relationships and will be discussed in a forthcoming paper.

The superfamily Tipuloidea is without doubt monophyletic (Hennig 1973, Wood & Borkent 1989), among others on the basis of larval characters. A phylogenetic scheme for the Tipuloidea was first framed by Alexander (1920), without a clear justification but apparently based on information from all life-stages. A different phylogeny was presented by the same author in 1927, based on the radial field of the wing. This study was criticized by Hennig (1954), who did not agree with some of Alexander's interpretations. A phylogeny based on pre-imaginal and imaginal characters of Palaearctic taxa was presented by Savchenko (1966, see also Savchenko 1979, 1983b), who concluded that, although Limoniidae and Cylindrotomidae are apparently sistergroups, there also exists a close relationship between Tipulidae and Limoniidae.

Both Alexander and Savchenko started from the concept that the three families within the Tipuloidea are monophyletic. This view was not followed by Hennig, especially not with respect to the Limoniidae, and he suggested that the Tipulidae might well be the sistergroup of part of the Limoniidae.

Oosterbroek (1986) proposed a new classification of the Tipuloidea into four families based on a preliminary study of larval and pupal characters. These four families and their sistergroup relations are: Cylindrotomidae – remaining Tipuloidea; Limoniidae – Eriopteridae + Tipulidae; Eriopteridae – Tipulidae. This classification is not confirmed by the results of the present study.

2. METHODS

Information about larval and pupal characters was available for those species of Limoniidae and Cylindrotominae mentioned in the index. Most characters are taken from the literature. Only a limited amount of characters could be studied from preserved material (see index). Valuable information about the morphology of larvae and pupae in Diptera, Nematocera and Tipuloidea is presented

by Alexander 1920 (Tipuloidea), Alexander & Byers 1981 (Tipuloidea), Anthon 1943a (Nematocera), Bangerter 1928-1934 (Tipuloidea), Bengtsson 1897 (Cylindrotominae), Brauns 1954a, 1954b (Diptera), Brindle 1960 (Tipulidae), 1967 (Limoniidae and Cylindrotominae), Byers 1961 (*Dolichozeina*), 1983 (*Chionea*), Chiswell 1955 (Tipulidae), Cook 1949 (Diptera), Courtney 1990, 1991 (Blephariceromorpha), Cramer 1968 (Tipuloidea), Crisp & Lloyd 1954 (Nematocera), Gelhaus 1986 (Tipulidae), Gérard 1968 (*Pilaria*), Giljarov (ed.) 1964 (Insects), Griffiths 1990 (Nematocera), Hennig 1948-1952, 1973 (Diptera), Hinton 1954-1968 (respiratory horns), Hynes 1958-1990 (Limoniidae), Krivosheina 1964 (Tipuloidea), 1969 (Diptera), Lenz 1920a (*Thaumastoptera*), Lindner 1959 (Limoniidae), McAlpine (ed.) 1981, 1989 (Diptera), de Meijere 1917 (Diptera), Oldham 1926 (*Pedicia*), Peterson 1960, 1965 (Insects), Peus 1952 (Cylindrotominae), Pokorný 1978 (*Eloephila*), Reusch 1988 (Limoniidae), Rogers 1926-1933 (Tipuloidea), Rozkosný 1980 (Tipulidae, Cylindrotominae), Rozkosný & Pokorný 1980 (Limoniidae), Smith 1989 (Diptera), Teskey 1981 (Diptera), Theowald 1957, 1967 (Tipulidae), Tokunaga 1930, 1933 (*Dicranomyia*), Vaillant 1951 (*Orimarga*), 1953 (*Symplecta*), Wiedenska 1987 (*Phylidorea*), Wirth & Stone 1956 (Diptera), Wolff 1922 (statocysts), Wood & Borkent 1989 (Nematocera), Wood 1952 (Tipuloidea).

Relationships are determined according to the phylogenetic principles as worked out by Hennig (1966), and as modified by Wiley (1981). Decisions about character polarities are based, as far as possible, on outgroup rules (Watrous & Wheeler 1981, Maddison et al. 1984).

The terminology largely follows Teskey (1981). The larval characters discussed and figured are those of the full grown, last larval stage, unless stated otherwise.

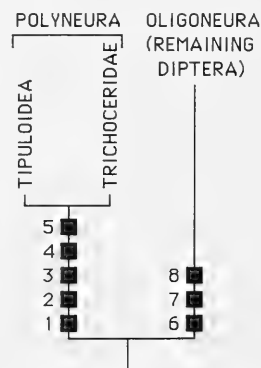


Fig. 1. Phylogeny of Tipuloidea, Trichoceridae and the remaining Diptera. For explanation see text.

3. OUTGROUPS

With respect to outgroup comparison, several levels can be recognized. The first level deals with the immediate sistergroup relation between Tipuloidea and other Nematocera, the second with the position of this sistergroup among the Nematocera, the third with the sistergroup of the Nematocera.

First level outgroups

In the literature the sistergroup of the Tipuloidea are either the Trichoceridae (winter crane flies; Hennig 1968, 1973; Griffiths 1990) or all other Diptera (Wood & Borkent 1989).

Tipuloidea and Trichoceridae as sistergroups (fig. 1)

Hennig (1968, 1973) united Tipuloidea and Trichoceridae in a monophyletic group (his suborder Polyneura or infraorder Tipulomorpha) on the basis of a number of synapomorphies. Wood & Borkent (1989) presented a critical analysis of these synapomorphies, and concluded that some are to be rejected or of little phylogenetic importance, while others are doubtfully homologous or in need of further investigation.

Arguments in favour of the monophyly of the Polyneura have been put forward by other authors as well (Rohdendorf 1964, Dahl & Alexander 1976, Dahl 1980, Griffiths 1990). The synapomorphies mentioned by Griffiths (1990) are (fig. 1): (1.) Reduction of male cerci, (2.) Development of gonopods from posterolateral zones of proliferation, (3.) Female cerci with single article, (4.) Only three branches of radial sector reaching wing margin, (5.) Forward displacement of distal section of M_{1+2} .

Tipuloidea and 'all other Nematocera' as sistergroups (fig. 2)

In Nannochoristidae, one of the important outgroups of the Diptera (see fig. 3), the larval mandible is provided with a separate sclerotized lobe (the lacinia mobilis of Pilgrim 1972). Among Tipuloidea a positionally similar structure is found only in Cylandrotominae (fig. 162), Tipulidae (figs. 179, 180) and the hexatomine genera *Pilaria* and *Ulomorpha* (fig. 61), the only two genera of Tipuloidea with a twofold mandible.

In their comprehensive analysis of the phylogenetic relationships among the Nematocera, Wood & Borkent (1989) tentatively considered the presence of a 'lacinia mobilis' in Nannochoristidae and

Tipuloidea a sympleisiomorphy and its absence in all other Nematocera a synapomorphy (fig. 2: character 1). However, the lacinia mobilis of Nannochoristidae and the separate sclerotized lobe of Cylandrotominae and Tipulidae most probably are not homologous. In Nannochoristidae the lacinia mobilis is already present in the first instar larva and the prosthecal brush of setae is situated basally (Pilgrim 1972: fig. 6). The separate sclerotized lobe of Cylandrotominae and Tipulidae is not yet present in the first instar larvae (fig. 161) and the prosthecal brush is situated at the apex (figs. 162, 179, 180).

The only remaining account of a 'lacinia mobilis' in Tipuloidea is the separated sclerotized lobe in *Pilaria* and *Ulomorpha* (fig. 61: pr). This lobe is not toothed as in Nannochoristidae. In the first stage larva it is already present, whereas the mandibles are not yet bifold (Gérard 1968 for *Pilaria*). The phylogenetic position of these two genera (fig. 6) and the very unique, highly specialized structure of the mandibles, which can close on itself like a 'pocket knife' (Crisp & Lloyd 1954), indicate that presence of a separated sclerotized lobe in *Pilaria* and *Ulomorpha* is most probably a synapomorphy. The same might be true for the lacinia mobilis of the Nannochoristidae because it is not present in the other Mecoptera.

Courtney (1990, 1991) assumed that the separate sclerotized lobe is homologous with the subbasal, thumb-like projection found in Psychodomorpha (see below, character 42). This subbasal projection, present in a number of Tipuloidea, occurs in Cylandrotominae together with the separate sclerotized lobe (fig. 162). Therefore, the presumed homology might be correct for other Nematocera, but can not be maintained for the Cylandrotominae and Tipulidae.

In his review of the paper by Wood & Borkent (1989), Griffiths (1990) hesitated to accept the absence of a separate sclerotized lobe as a synapomorphy for all Nematocera except Tipuloidea. In the present study, the separate sclerotized lobe is interpreted as a synapomorphy for Cylandrotominae and Tipulidae (chapter 4: character 22). The phylogenetic position of these taxa (fig. 4) does not favour the assumption that this character belongs to the groundplan of the Tipuloidea.

It can be concluded that character 1 of figure 2 is a questionable synapomorphy for all Nematocera except Tipuloidea. During the present study, a sistergroup relation between the Tipuloidea and all other Nematocera could not be established on the basis of other synapomorphies.

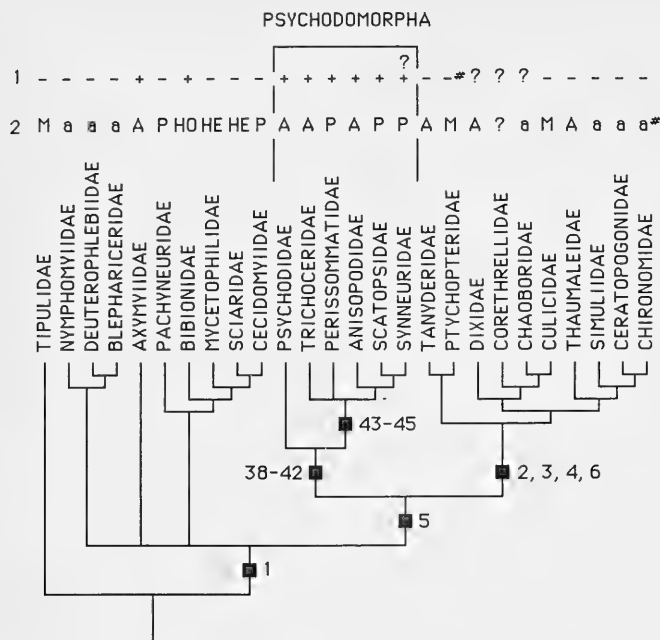


Fig. 2. Phylogeny of the Nematocera after Wood & Borkent (1989). Row 1, referring to the pupal leg sheaths and row 2, referring to the respiratory system, are added. - Row 1: - pupal leg sheaths side by side, + pupal leg sheaths superimposed, *at least two pairs of leg sheaths side by side (Ptychopteridae). - Row 2: M metapneustic, a apneustic, A amphipneustic, P peripneustic, HO holopneustic, HE hemipneustic, * except *Archaeochlus* (Chironomidae).

Second level outgroups

Oligoneura sensu Hennig (1968, 1973) (fig. 1)

Hennig (1968, 1973), following Lindner (1949), divided the Diptera in two suborders, Polyneura (Tipuloidea plus Trichoceridae) and Oligoneura (the remaining Diptera). Oligoneura can be considered monophyletic on the basis of the following characters (fig. 1). (6.) Arolium absent, replaced by a flap-like empodium, (7.) A2 rudimentary or absent, (8.) Base of veins M and R connected by an oblique crossvein.

Characters 6-8 were discussed by Wood & Borkent (1989), who concluded that all three characters are in need of further investigation and that other evidence to corroborate the monophyly of the Oligoneura seems to be lacking. After a detailed study of the fifth tarsomere throughout the Diptera and a number of Mecoptera, Röder (1984) concluded that character 6 is a synapomorphy for the Oligoneura.

Larval mouthparts in Tipuloidea do not show the striking similarities as present between Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae, discussed in more detail in the next chapter. These similarities must be interpreted as belonging to the groundplan condition of the Nematocera, if the phylogeny presented in fig. 1 is correct. A similar conclusion was reached by Edwards (1926, 1928), Anthon (1943a), Hennig

(1954), Dahl & Alexander (1976). Edwards (1928) was unable to discover anything among the adults which would suggest that *Trichocera* should be included in the Anisopodidae ('In almost every respect the adults of the genus [*Trichocera*] are typical Tipulids ... It seems probable that we should regard *Trichocera* as a primitive genus which in its larvae at least has retained many of the characters of the ancestors of the Tipulidae, and its resemblances to the Anisopodidae are probably due to this fact').

Some of the characters of the larval mouthparts are also present in Ptychopteridae and Tanyderidae. Therefore, on the basis of fig. 1, these families together with Psychodidae, Anisopodidae and Scatopsidae are to be regarded as second level outgroups.

Psychodomorpha sensu Wood & Borkent (1989) (fig. 2)

Keilin (1912) was the first to decide that on larval characters *Trichocera* should be separated from the Tipulidae s.l. Wood & Borkent (1989) analysed these larval characters in much detail, with emphasis on the larval mouthparts. Several of these mouthpart characters were interpreted by Wood & Borkent as synapomorphies (fig. 2: characters 38-45), uniting Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae in the infraorder Psychodomorpha, together with Perissommatidae and Synneuridae.

Griffiths (1990) stated that the synapomorphies between Tipuloidea and Trichoceridae (fig. 1: characters 1-5) can not easily be dismissed. Therefore, in his view, the Tipuloidea are to be included in the Psychodomorpha as sistergroup of the Trichoceridae, stating that this: 'is reconcilable with Wood & Borkent's justified emphasis on the synapomorphies between the larval head structure of Trichoceridae and that of other Psychodomorpha, if we assume that the considerable diversity of head structures shown by the larvae of Tipulidae s.l. represents a transformation series from a groundplan structure similar to that of *Trichocera*'.

According to the above, the other families included in the Psychodomorpha, especially Psychodidae, Anisopodidae and Scatopsidae, are to be considered second level outgroups.

Synapomorphies for the Psychodomorpha

The conclusion about second level outgroups is more or less the same for both phylogenies presented in fig. 1 and fig. 2. In both instances, characters of the larvae of Tipuloidea must be interpreted as representing a transformation from a groundplan structure similar to that of Trichoceridae, Psychodidae, Anisopodidae and Scatopsidae. Whether this interpretation is correct can be determined by comparing the larval characters of Tipuloidea with the synapomorphies listed by Wood & Borkent (1989) for Psychodomorpha, Ptychopteromorpha and Culicomorpha (fig. 2: character 5) and Psychodomorpha (fig. 2: characters 38-45):

Character 5 (Wood & Borkent): 'Epicondyle displaced medially and hypocondyle displaced laterally, with the mandibles operating obliquely or vertically'. – As discussed below (character 41), this synapomorphy is probably of little phylogenetic significance. Courtney (1990, 1991) accepted it with some reservation to support the monophyly of Blephariceromorpha and Psychodomorpha.

Character 38: 'Labrum conical or wedge-shaped, rounded, or pointed anteroventrally, more or less covered apically and ventrally with backwardly projecting hairs'. – In many Tipuloidea the labrum is broadly rounded and especially ventrally covered with backwardly projecting hairs. A distinctly narrow labrum is found in Eriopterinae (figs. 13, 19) and Cylindrotominae. The plesiomorphic condition, 'labrum flattened dorsoventrally and usually bilobate' is present in most Hexatominae, Limoniinae and Tipulidae (e. g. fig. 73). The apomorphic condition is present also in Blephariceridae, Axymyiidae and Thaumaleidae. In Psychodomorpha some Psychodidae (*Phlebotomus*, *Trichomyia*) and the Synneuridae exhibit the plesiomorphic condition.

Character 39: 'Premandible in the form of a rounded or oval sclerite with a comb-like row of evenly spaced, anteriorly projecting teeth, presumably operated by the labral retractor muscles to comb the mandible or maxilla'. – In Tipuloidea premandibles as in Psychodomorpha are absent. Especially in Hexatominae, however, the epipharynx is provided with two relatively large sclerotized plates situated caudal of the epipharyngeal bar (fig. 73; see also Pokorný 1978: figs. 14-16 for *Eloeophila* and Wiedenska 1987: figs. 4-5 for *Phylidorea*). Positionally these plates might be homologous to the premandibles. The same applies for the structures figured by Vaillant (1953: fig. 4) for the eriopterine genus *Symplecta*. Among Psychodomorpha, the apomorphic condition is not present in the anisopodid genus *Olbiogaster* (Keilin & Tate 1940, Anthon 1943b), the psychodid genus *Trichomyia* and the Synneuridae (Wood & Borkent 1989). Wood & Borkent (1989) considered the shape of the premandibles as 'one of the most convincing pieces of evidence of the monophyly of the infraorder [Psychodomorpha]', although they did not indicate which taxa exhibit the plesiomorphic condition ('premandibles in the form of a simple, unadorned sclerite, serving only as a point of insertion of the labral retractor muscles'). Blephariceromorpha, Axymyiidae and Bibionomorpha apparently lack premandibles except for Mycetophilidae (s.l.) and Sciaridae. Premandibles in the two last-mentioned families are not necessarily homologous with those present in Psychodomorpha (Goetghebuer 1925, Edwards 1926, Plachter 1979). Edwards (1926) and Courtney (1990) supposed that premandibles possibly arose as a groundplan feature of Diptera larvae. This might be the correct interpretation because this character should be placed at a lower level in the phylogeny of figure 2, namely at the same position as character 5 (see also Courtney 1991: fig. 4b). This lower position is apparent from the statement by Wood & Borkent (1989) that the premandible of the Psychodomorpha represents the plesiomorphic condition with respect to the apomorphic premandibles of Ptychopteromorpha and Culicomorpha (fig. 2: character 3).

Character 40: 'Torma articulated with the dorsal labral sclerite'. – This character is present in several groups of Tipuloidea, most distinctly in the larger Tipulidae (fig. 174), but observed also in *Dactylolabis* and several Limoniinae. Articulating tormae are mentioned in the literature for *Cryptolabis* (Eriopterinae, Hynes 1963), *Pedicia* (Pediini, Wardle & Taylor 1926), *Dicranomyia* (Limoniinae, Tokunaga 1933), and similar structures are figured and described for *Thaumastoptera* (Limoniinae, Lenz 1920a). Cook (1949) identified the

premandibles in *Holorusia*, but given the position of these sclerites it is likely that they are the tormae (fig. 174). According to Wood & Borkent (1989) this character might represent a synapomorphy at the same position in figure 2 as character 5, whereas Courtney (1990, 1991) unites Blephariceromorpha and Psychodomorpha on the basis of the presence of articulated tormae in Blephariceromorpha.

Character 41: Mandibular movement 'in a nearly vertical plane as a result of a shift in position of the condyles, with the mandibles striking the anterior edge of the hypostoma or hypostomal teeth'. – An oblique or vertical orientation of the larval mandibles is present in all Eriopterinae, Hexatomiinae, *Ula* and sometimes Pediciini (chapter 4: character 10). The mandibles move in a horizontal or nearly horizontal plane in all other Tipuloidea, except Cylindrotomiinae. In this subfamily the mandibles move horizontal in first stage larvae and almost vertical in second stage to full grown larvae (Bengtsson 1897, Alexander 1920, Peus 1952). Among Nematocera as a whole this character is subject to homoplasy and probably of questionable value in phylogenetic interpretations (Courtney 1990, 1991). As stated by Wood & Borkent (1989: character 5), the positions of the mandibular articulation points have probably shifted more than once and reversals have undoubtedly occurred. The orientations of the mandibles vary in the Psychodomorpha (horizontal in the psychodid subfamilies Trichomyiinae (Wood & Borkent 1989) and Bruchomyiinae (Satchell 1953), obliquely in Perissommatidae), Ptychopteromorpha (Tanyderidae horizontal, some Ptychopteridae vertical), and Culicomorpha (horizontal in *Stenochironomus*). In most Bibionomorpha the mandibles move in a horizontal plane but in Mycetophilidae (s.l.) the mandibles operate in a semi-circular way (Plachter 1979: 'halbkreisförmig').

Character 42: 'Mandible in the shape of a chela with a small, subbasal, thumb-like projection curving toward the apex of the mandible' (figs. 9, 10). – Mandibular shapes are rather varied within Tipuloidea. A small subbasal projection curving toward the apex is present in a few Eriopterinae (fig. 11; see also chapter 5: character 56) and in some species of *Dactylolabis* (fig. 128). Within Psychodomorpha the apomorphic condition is not found in the psychodid genera *Bruchomyia* and *Phlebotomus* (Satchell 1953), and is less distinct in Perissommatidae (Wood & Borkent 1989) and the scatopsid subfamily Ectaeiinae (Laurence 1953).

Character 43: 'Apical portion of mandible separated from the base by a less strongly sclerotized line of weakness'. – Bifold mandibles of a very characteristic and completely different shape than in Psy-

chodomorpha (figs. 9, 10) are present in the highly specialized hexatomiine genera *Pilaria* and *Ulo-morpha* (fig. 61). In all other Tipuloidea the apical portion is solidly fused with the base of the mandible (e. g. fig. 11). According to Anthon (1943a) and Hennig (1973) bifold mandibles probably belong to the groundplan condition of the Diptera and after Lindner (1959) its occurrence in Tipuloidea must be interpreted as a reversal to the plesiomorphic condition. If apomorphic, this character unites Psychodomorpha and Blephariceromorpha (Courtney 1990, 1991) and possibly also Ptychopteromorpha (Tanyderidae: Anthon 1988: *Mischoderus*; Ptychopteridae: Anthon 1943a, Wood & Borkent 1989). A bifold mandible is also present in one subfamily of Psychodidae (in Psychodinae, where it is similar to the other Psychodomorpha). In the other three subfamilies of Psychodidae (Bruchomyiinae, Phlebotomiinae, and Trichomyiinae) the mandible is simple (Satchell 1953, Quate & Vockeroth 1981). The apomorphic condition could not be ascertained for the Perissommatidae and is apparently absent in the Synneuridae (Wood & Borkent 1989) and the scatopsid subfamily Ectaeiinae (Laurence 1953).

Character 44: 'Cardo reduced, mainly membranous'. – The description of this synapomorphy by Wood & Borkent (1989) does probably not refer to the cardo itself, which is a well developed sclerite in several Anisopodidae, Trichoceridae and Scatopsidae (see Anthon 1943a: figs. 55–60, Krivosheina 1969), but to the pattern of 'backwardly pointing setae forming a characteristic pattern, unique in the Diptera', situated on the membranous area between the cardo and the maxillar lobes. These backwardly pointed setae are absent in Tipuloidea, but also in the anisopodid genera *Mycetobia* and *Olbiogaster* (Keilin 1919, Anthon 1943a, 1943b, Keilin & Tate 1940, Krivosheina 1969), whereas similar setae are present in *Philosepedon* (Psychodidae) and *Ptychoptera* (Ptychopteridae) (Anthon 1943a). A membranous cardo occurs in Nannochoristidae and Blephariceromorpha and is considered further evidence for the sistergroup relation between Blephariceromorpha and Psychodomorpha by Courtney (1990, 1991). In Tipuloidea the cardo is usually well developed and of the same shape as in many other Nematocera (see also Cook 1949). Little information is available for Eriopterinae and Hexatomiinae, but in *Cryptolabis* (Hynes 1963) and *Pseudolimmophila* (fig. 58) the cardo lies parallel to the ventral anterior margin of the genae, as in the first and second level outgroups. In *Ula* and the members of the *Dactylolabis*-Tipulidae lineage of figure 4, only the proximal end of the cardo is near to the anterior margin of the genae (e. g. figs. 160, 173). This character, which can not be interpreted

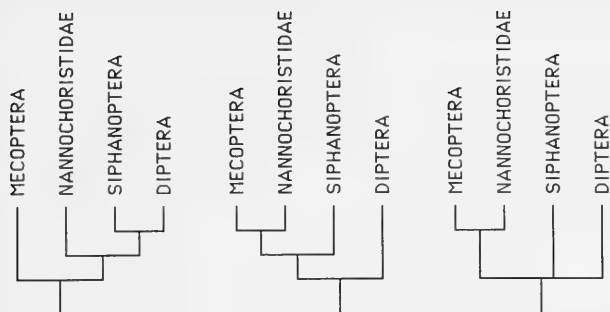


Fig. 3. Phylogenetic arrangements for the Antliophora. – A, after Wood & Borkent (1989); B and C, after Willmann (1989) and Griffiths (1990).

for the reduced cardo of Pediciini (fig. 100), seems to be closely associated with the orientation of the anterior margins of the genae (chapter 4: character 5).

Character 45: 'Maxillary palpus reduced to a disc-like sclerotized ring'. – According to Wood & Borkent (1989), in the Trichoceridae, Perissommatidae, Scatopsidae, and Anisopodidae, the maxillary palpus is flush with the surface of the maxilla, recognizable only by a ring of chitin surrounding the sensilla. This type of maxillary palpus is found in Eriopterinae (figs. 15, 23), Hexatomiinae, Pediciini (the two last-mentioned taxa with the outer maxillary lobe elongated and the sensilla situated near or at the apex, figs. 68, 100), *Ula* (fig. 113) and *Dactylolabis*. In other Tipuloidea the sclerotized ring surrounding the sensilla is cylindrical and usually well developed (fig. 121; see also chapter 4: character 12). A reduced maxillary palpus occurs also in Cecidomyiidae (Mamaev & Krivosheina 1965), Mycetophilidae (s.l.) and Sciaridae (Plachter 1979).

Conclusions

The above comparison shows that a number of larval head characters of Tipuloidea, especially in Eriopterinae and Hexatomiinae, correspond to the synapomorphies listed by Wood & Borkent (1989) for the Psychodomorpha. From this it can be concluded that Edwards (1926, 1928) and Griffiths (1990) were probably right when they stated that larval characters of Tipuloidea are to be interpreted as a transformation series from a groundplan structure similar to that of *Trichocera*.

It is also apparent that several of the synapomorphies listed by Wood & Borkent (1989) for the Psychodomorpha are not present in all representatives of this infra order and/or are present in other families of Nematocera as well. Some of these characters, therefore, must be regarded

groundplan structures for a grouping of nematoceran families larger than the Psychodomorpha (as worked out for the Blephariceromorpha by Courtney 1990, 1991), or for even all Nematocera. From this it follows that some of the Psychodomorpha families might belong to the most basal lineages of the Diptera. This latter observation is in agreement with the hypothesis by Anthon (1943a) that the presence of a transverse tentorium represents the primitive condition, as found in primitive insects, Mecoptera (incl. Nannochoristidae), Siphonaptera, and among Psychodomorpha in Anisopodidae and Perissommatidae. Wood & Borkent (1989: 1356), stated that it is difficult to refute the hypothesis that the anisopodid larva represents one of the most primitive types of dipterous head, but on the other hand prefer to suppose that the transverse tentoria of Anisopodidae and Perissommatidae are a de novo development, apparently not present in the other families of Diptera (see also chapter 4: character E).

Third level outgroups (fig. 3)

Diptera, Mecoptera (including Nannochoristidae) and Siphonaptera are usually united in the Antliophora. Various sistergroup relations have been proposed (fig. 3) but the matter is still open to debate (reviews in Hennig 1981, Willmann 1989, Wood & Borkent 1989 and Griffiths 1990). For the present study, outgroup comparison is largely based on characters of Mecoptera including Nannochoristidae (Byers 1963, Kaltenbach 1978, Pilgrim 1972, Steiner 1930).

4. TIPULOIDEA

Introduction

On the basis of the available information the Tipuloidea can be divided in at least two, appar-

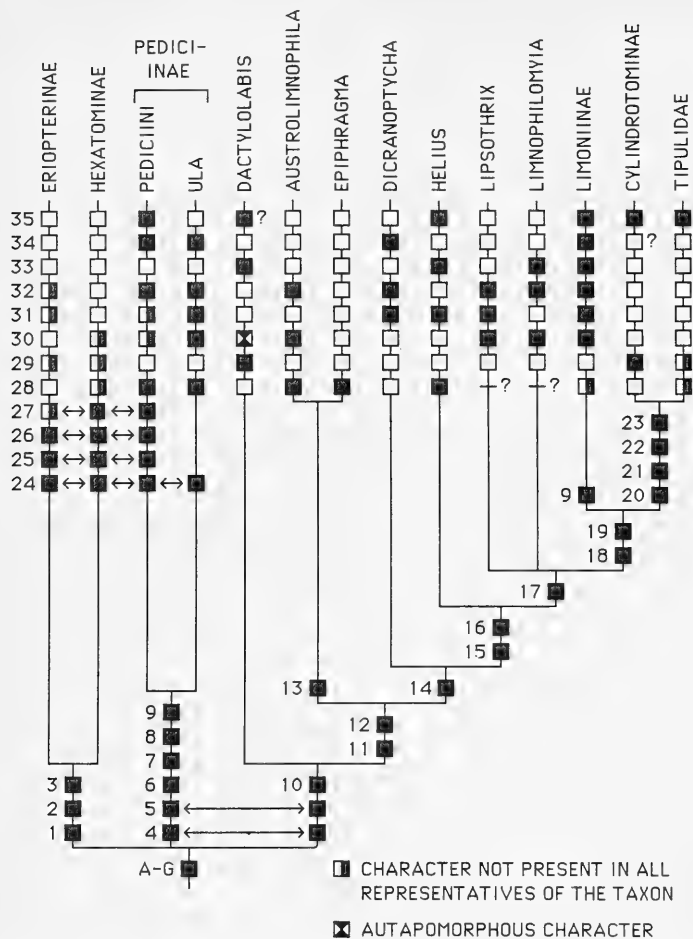


Fig. 4. Phylogeny of the major groups of Tipuloidea.

ently monophyletic groups (fig. 4), the Eriopterinae-Hexatomininae lineage and the *Dactylolabis*-Tipulidae lineage. These two lineages and the Pediciinae are placed at a basal trichotomy. Characters 4-5 point in the direction of a sistergroup relation between the Pediciinae and the *Dactylolabis*-Tipulidae lineage, character 24 to such a relation between the Pediciinae and the Eriopterinae-Hexatomininae lineage. The monophyly of the Pediciinae, based on characters 6-9, is not corroborated by characters 25-27.

Pediciinae are the only Tipuloidea with hairy eyes in the adults, without doubt a symplesiomorphic character. Therefore, it might be expected to find the Pediciinae at the most basal position, as sistergroup of the Eriopterinae-Hexatomininae plus *Dactylolabis*-Tipulidae lineages. An indication for resolving the trichotomy in this way is the shape of the prementum in Pediciinae (see character 6). It also appears that the pharynx and oesophagus of

Pediciini and *Ula* (detailed description in Miall 1893, Oldham 1926, Lindner 1959) show a certain resemblance to the pharyngeal filter apparatus of Trichoceridae and several second level outgroups (detailed description in Anthon 1943a). Very little information is available for the pharynx and oesophagus of other Tipuloidea but a pharyngeal filter apparatus as in *Ula* (Lindner 1959) and perhaps also Pediciini is not present in *Chionea* (Eriopterinae, Byers 1983), *Pilaria* and *Hexatoma* (Hexatomininae, Cook 1949, Gérard 1968), *Antocha* and *Limonia* (Limoniinae, Sinclair, pers. comm.) and *Holorusia* (Tipulidae, Cook 1949).

In the text below, Pediciinae, Cylindrotominae and Tipulidae (s. str.) have the same meaning as the corresponding but sometimes differently ranked taxa in the current systematic literature (Hutson 1980, Dienske 1987, Oosterbroek 1989, Savchenko 1989, Savchenko et al. 1992). On the basis of larval and pupal characters, Eriopterinae

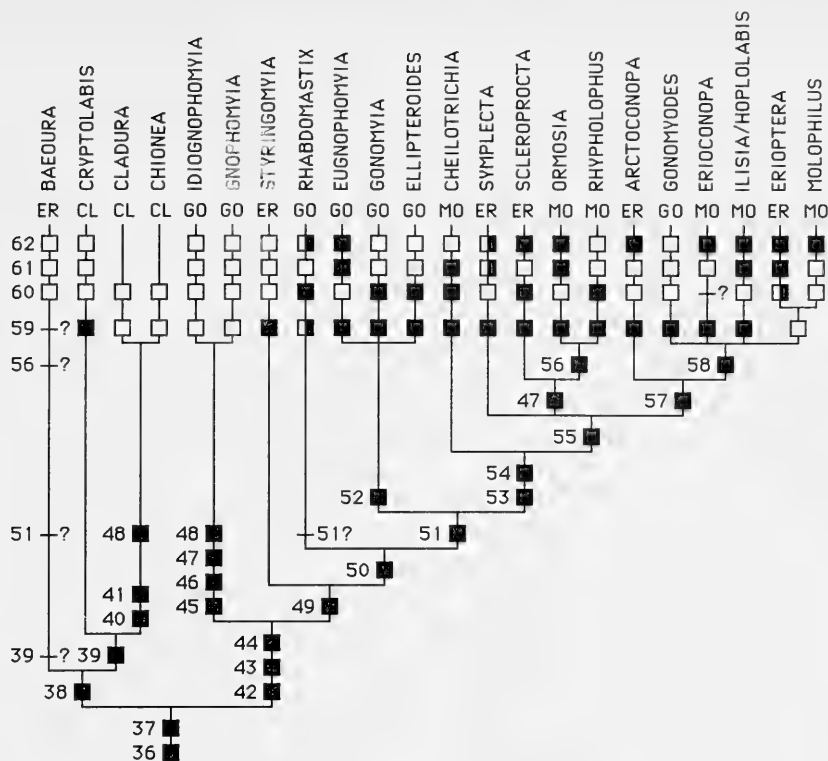


Fig. 5. Phylogeny of the Eriopterinae. The genera are generally considered to belong to the tribes abbreviated as CL: Cladurini, ER: Eriopterini, GO: Gonomyiini, MO: Molophilini.

and Hexatomiinae are treated in a more restricted sense, the former without the genera *Conosia*, *Lipsothrix* (conform Rogers & Byers 1956) and *Limnophilomyia*, the latter without *Dactylolabis*, *Austrolimnophila*, *Epiphragma* and *Atarba* (discussed in chapter 9), but including *Conosia* (conform Alexander 1972, Oosterbroek 1989). Furthermore, the subfamily Limoniinae does not include *Dicranoptycha* and *Helius*.

Throughout the text reference is made to 'lower' and 'higher' Eriopterinae and Hexatomiinae. In both subfamilies 'lower' refers to genera with a more or less compact head capsule (in Eriopterinae the genera *Baeoura* to *Gnomophomyia* in the left part of figure 5, in Hexatomiinae the genera *Paradelphomyia* and *Pseudolimnophila*), and 'higher' to genera with a more reduced head capsule.

In the next chapters the following characters will be discussed:

Larval characters: General: 26, 34, 36, 40, 54, 60, 68, 76, 82, 99. – Creeping welts: 29, 30, 48, 79, 84, 91, 95, 103. – Spiracles and spiracular field: A, 20, 41, 43, 44, 52, 55, 57, 58, 61, 62, 80, 87, 88, 90, 94, 101, 102, 104 (see also below, Spiracular lobes). – Anal papillae: 47, 63. – Head capsule, general:

B, C, D, E, 1, 2, 3, 5, 8, 17, 19, 21, 24, 25, 49, 67, 69, 72, 105 (see also below: Head capsule). – Labrum: 13, 39, 64. – Antenna: 7, 51, 97, 98. – Maxilla: 12, 18, 27, 65, 71, 83. – Mandible: 10, 22, 56, 66, 70, 78, 89. – Hypopharynx and prementum: 6, 15, 16. – Hypostoma: G, 11, 23, 35, 59, 85, 86, 93.

Pupal characters: General: 9. – Palpsheaths: 42. – Thorax: F, 33, 37, 50. – Respiratory horns: 38, 46, 73, 74, 77 (see also below: Respiratory horns). – Abdomen: 4, 14, 53, 75, 81, 92. – Creeping welts: 31, 32, 45, 96, 100.

Head capsule

Many Tipuloidea possess a more or less compact head capsule that is ventrally largely open, with distinct incisions which divide the genae in externo- and interno-lateral parts (fig. 14: elp, ilp), and with the frontoclypeal apotome always distinctly shorter than the head capsule (e. g. figs. 14, 119). This character might represent a synapomorphy because the frontoclypeal apotome is of about the same length as the genae in most other Nematocera (incl. *Trichocera*). However, in the related orders and especially the Mecoptera, the

apotome can be shortened as well.

In groups with a compact head capsule, the head capsule of the first stage larva is shaped as in figure 112, with a dorsal plate, the frontoclypeal apotome and two lateral plates, the genae. During the several larval stages the head capsule grows larger with distinct growth lines bordering the genae (e. g. fig. 139; detailed description for *Limonia* in Lindner 1959). These growth lines apparently do not occur in other Nematocera, except for the tanyderid genus *Mischoderus* (Anthon 1988).

Among Tipuloidea the primitive type of head capsule is most probably as in *Ula* (fig. 116; *U. mollissima*, figs. 110, 111, excepted), *Dactylolabis*, *Austrolimnophila* (figs. 119, 120), *Epiphragma*, *Dicranoptycha* (fig. 131) and *Helius* (fig. 134), with distinct coronal and frontal sutures as in the outgroups and with the posterior part of the genae less deeply incised.

A similar head capsule but with the internolateralia united with the frontoclypeal apotome is found in *Limnophilomyia*, *Lipsothrix*, Limoniinae (fig. 140), Cylindrotominae and Tipulidae (fig. 173; see also character 17). In this type of head capsule the frontal sutures are usually obliterated but in Tipulidae they appear as narrow hyaline ribbons.

The massive head capsule of Pediciini (figs. 93, 94) is discussed under character 8. Extreme reduction of the head capsule is typical for the higher Eriopterinae (figs. 13-15; see also character 49) and higher Hexatominæ (figs. 66-69; see also character 67). These specialized head capsules are termed dissected and consist mainly of elongate rods which are very flexible and 'work to some degree like the ribs of an umbrella ... undoubtedly an adaptation for rapid burrowing for such a head can be pushed into very narrow crevices' (Crisp & Lloyd 1954). In higher Hexatominæ flexibility of the head capsule is associated with their method of feeding as well (Crisp & Lloyd 1954, Lindner 1959).

Spiracular lobes

Full grown larvae of many Tipuloidea possess four distinct spiracular lobes, sometimes with a smaller or vestigial dorsal lobe (e. g. figs. 72, 78). In Tipulidae and Cylindrotominae six lobes are present (figs. 164, 177; see also character 20). Five more or less identical lobes or, when reduced, sclerites are found in most genera of Eriopterinae (e. g. fig. 39; see also character 43), in several species of *Ula* (fig. 118), in *Austrolimnophila* (fig. 123) and in *Helius* (fig. 136). In Eriopterinae the number of spiracular lobes can also be four (*Baeoura* fig. 27, *Cryptolabis* figs. 28, 29), seven (*Styringomyia* Hynes 1990: fig. 1, *Gonomyodes* Hynes 1969b: fig. 1) or nine (*Ellipteroides* fig. 35). A peculiar char-

acter of the spiracular field among Eriopterinae is the presence of heavily sclerotized spines in *Arctoconopa* and *Rhabdomastix* (fig. 43).

Only two ventral lobes are present in Pediciini (figs. 105-108) and the limoniine genus *Antocha*. Very reduced or no spiracular lobes at all are found among genera of Eriopterinae (*Cladura*, *Chionea* fig. 32, *Hesperoconopa*, *Neolimnophila*, *Rhabdomastix*), Hexatominæ (some species of *Hexatoma* and *Limnophila*), *Austrolimnophila* (fig. 123), *Limnophilomyia*, *Elephantomyia aurantiaca* (fig. 169), and genera of Limoniinae (figs. 141, 142; see also character 104).

Several authors (Peus 1952, Lindner 1959, Brindle 1967) suggested that the plesiomorphic condition is six lobes in Cylindrotominae and Tipulidae, and five in the Limoniidae s.l. For several reasons it is assumed here that the plesiomorphic condition in Tipuloidea is four relatively short lobes:

(a) No distinct conclusions can be drawn on the basis of outgroup comparison, but there are four distinct and relatively short spiracular lobes in *Trichocera*. In other Nematocera the number of spiracular lobes ranges from zero to five and they are never as elongate as in lower Eriopterinae and Hexatominæ. In the related orders a distinct spiracular field does apparently not occur.

(b) The first instar larvae of most Tipuloidea possess, as far as is known at the moment, four lobes or, when the lobes are reduced, four sclerites (fig. 117), even if the full grown larva does possess five or six lobes (fig. 118; see also figures in Peus 1952, Lindner 1959, Reusch 1988). The development of the dorsal lobe takes place during larval growth. This sometimes results in five more or less identical lobes (*Ula* fig. 118, *Helius* fig. 136), but usually the dorsal lobe is much smaller than the other four (figs. 72, 78). It is apparently only in the higher Eriopterinae that first stage larvae of some genera already possess five spiracular lobes and/or sclerites as in the full grown larvae (fig. 42; see also figures in Lindner 1959, Okely 1979, Reusch 1988).

(c) Pupae of a great number of Tipuloidea have blunt or acutely tipped lobes on the dorsum of tergite 8. These lobes develop in the spiracular lobes of the larva during pupation. In part of the Tipuloidea with five or six spiracular lobes, the number of pupal lobes is nevertheless four. Moreover, in cases where the larvae have their spiracular lobes strongly reduced or lost, there are still four distinct lobes in the pupa (for example *Austrolimnophila*, *Tanyptera*, *Dendrotipula*). It is only in some species of Hexatominæ and in a number of Eriopterinae that the pupae possess a pentagon of five lobes on the dorsum of tergite 8 (figs. 49, 55, 56).

Respiratory horns

Mesothoracic respiratory horns are absent in pupae of Mecoptera and only weakly developed in *Trichocera* and several second level outgroups. They are present in most Tipuloidea and a number of other nematoceran families (Brauns 1954b). The groundplan condition in Tipuloidea is elongate, more or less cylindrical (figs. 86-90) or somewhat flattened respiratory horns, as in most Eriopterinae and Hexatomininae, *Ula*, *Dactylolabis*, *Austrolimnophila*, *Epiphragma*, *Helius*, several Limoniinae, Cylindrotominiinae and most Tipulidae.

The respiratory gill function (plastron respiration) of the mesothoracic horns is described in detail by Hinton (1955-1968).

Various deviations from the apparent groundplan condition are:

Earshaped (figs. 48, 154). – *Gnophomyia*, *Idiog-nophomyia*, *Gonomyia* and *Ellipteroides* (sometimes with a basal stem, fig. 51), *Euphyllidorea*, *Phyllidorea*, *Tricyphona*, *Lipsothrix*, *Elliptera*, *Ori-marga*, most Limoniinae.

Branched (figs. 158, 159). – *Antocha* (*Antocha*) 8-branched, *Antocha* (*Orimargula*) 5- to 6-branched, *Dicranomyia trifilamentosa* 3-branched.

Acute (figs. 47, 53, 155). – *Austrolimnophila*, *Epiphragma*, some Erioptera and *Hexatoma* species. Species with acute respiratory horns are able to insert them in the roots of plants to obtain oxygen from the gas spaces of these plants (fig. 53; described in detail by Houlihan 1969).

Very elongate with the tips split into divergent flaps (figs. 88, 91). – *Pseudolimnophila*, *Pilaria*, *Ulomorpha* and *Polymera*. The apical flaps are pulled apart when the tips of the horns reach the water surface from below, enabling the pupa to float. The emergence of the adult from a floating pupa of *Polymera* is described by Rogers (1933). Further details on the structure of the horns and their functioning in floatation are given by Hinton (1954) for *Pseudolimnophila*.

Reduced or absent (fig. 46). – *Baeoura*, *Cryptolabis*, *Chionea*, *Cladura*, *Hesperoconopa*, *Dicranoptycha*, *Pedicia*, some *Elephantomyia* species.

Monophyly of the Tipuloidea

Synapomorphies for the Tipuloidea are (fig. 4):
A. Larvae metapneustic

Larvae of Tipuloidea are metapneustic, having functional spiracles on the last abdominal segment only. Exceptions are the apneustic larvae of *Antocha*, *Hesperoconopa dolichophallus*, *Dicranomyia capicola* and possibly *Aphrophila neozelandica*. Sometimes spiracles are present on the pleura of abdominal segments 1-7, but they are not func-

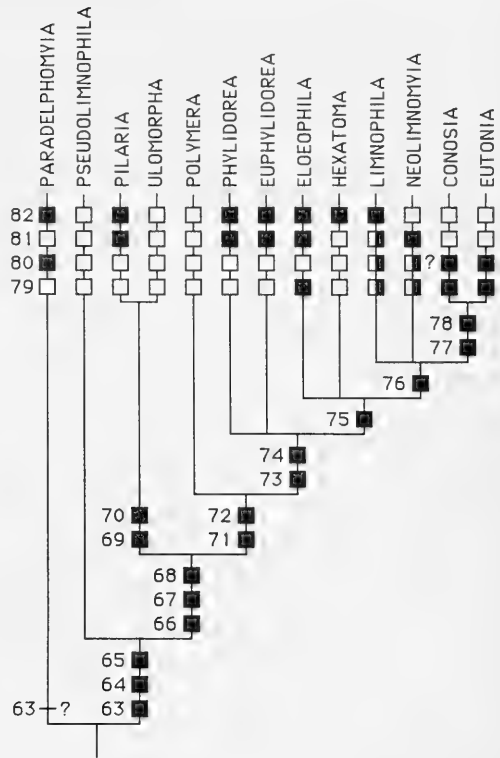


Fig. 6. Phylogeny of the Hexatomininae.

tional and most distinct shortly after ecdysis (Alexander 1920, Lindner 1959).

The larval respiratory system of Mecoptera is peripneustic, in Nannochoristidae apneustic (first three larval stages) or hemipneustic (full grown larva). Nematocera are usually peri-, amphi- or apneustic (fig. 2), the only other metapneustic forms are found in Ptychopteridae and Culicidae. According to Keilin (1944), first stage larvae of apparently all Diptera are metapneustic ('The metapneustic system appears as the first stage of development in all respiratory systems except the apneustic one' (Keilin 1944: p. 31). Preservation of the metapneustic condition in full grown larvae, as in Tipuloidea, therefore, could represent the plesiomorphic condition. On the other hand 'metapneustic and amphipneustic forms which are adapted to a partially submerged condition of life are more specialized and are derived from the primitive terrestrial polypneustic form' (Keilin 1944: p. 31; see also Hinton 1947: p. 466, Wood & Borkent 1989: p. 1342).

B. Larvae hemicephalic

Larvae of Tipuloidea are hemicephalic, the head

capsule can be retracted into the body. This character is also present in the Brachycera. The plesiomorphic condition in Diptera is without doubt an eucephalic head capsule, as in almost all other Nematocera and related orders. In the nematoceran family Axymyiidae the head can be partly retracted into the body as well (Mamaev & Krivosheina 1966). According to Teskey (1981), the hemicephalic condition in Tipuloidea does not imply a vertical orientation of the mandibles as in the Brachycera. It is assumed here that within the Tipuloidea a horizontal orientation is derived from an oblique orientation (see character 10).

C. Ventral margins of the genae extending far anteriorly

Correlated with the hemicephalic condition is reduction of the larval head capsule, whereby in all Tipuloidea the ventral margins of the genae are letting free a large portion of the ventral floor of the head (ventral part of occipital foramen distinctly extended anteriorly). In the related orders and almost all other Nematocera the ventral floor is largely closed or the ventral contact of the genae is situated not further anteriorly than about halfway the length of the genae, some Mycetophilidae (s.l.) excepted.

D. Genae posteriorly incised

Reduction of the larval head capsule is also exemplified by distinct incisions which divide the genae in externo- and interno-lateralia (fig. 14: elp and ilp). These incisions are not present in the related orders or in other Nematocera except for Axymyiidae (Mamaev & Krivosheina 1966). It is noteworthy that in *Trichocera* the posterior margin of the genae is sharply invaginated at the same position as the incisions of Tipuloidea (see Anthon 1943a: 'mf' in fig. 6 & 8). In some species of *Ula* and in Pediciini the incisions are hardly developed (figs. 93, 110).

E. Tentorium reduced

A complete tentorium, consisting of tentorial arms and a transverse tentorium is considered to belong to the groundplan of the Diptera by among others Anthon (1943a), Hennig (1973), Teskey (1981). Tentorial arms are present in *Trichocera* and in several but not all families of Nematocera and Brachycera. In addition to the tentorial arms a transverse connection is apparently restricted to Anisopodidae and Perissomatidae (Wood & Borkent 1989), although it is described as well for the nematoceran families Bibionidae (Perraudin 1961), Mycetophilidae (s.l.) (Plachter 1979) and Dixidae (Nowell 1951). In Tipuloidea the transverse connection is absent and the tentorial arms

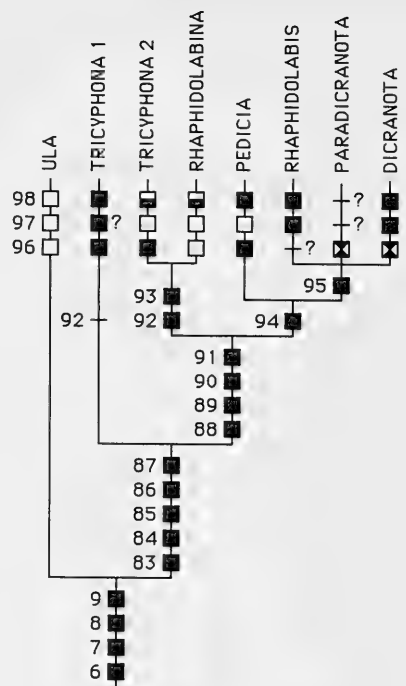


Fig. 7. Phylogeny of the Pediciinae.

are extremely reduced (Lindner 1959: fig. 9).

F. Pupal legs sheaths side by side

In all Tipuloidea the pupal leg sheaths are lying side by side. This character must be considered a weak argument for the monophyly of the Tipuloidea because several other nematoceran families have the leg sheaths side by side as well. Superimposed leg sheaths are nevertheless found in all families of the Psychodomorpha (sensu Wood & Borkent 1989) and also in Axymyiidae and Bibionidae (fig. 2).

G. Hypostoma anteriorly toothed and consisting of central and lateral parts

The hypostomal region of Tipuloidea is rather diverse. All taxa, except higher Hexatominae, the majority of Eriopterinae and some species of *Elephantomyia* (see chapter 9), possess a distinctly toothed hypostoma (e. g. fig. 131). Most lower Eriopterinae also possess a toothed hypostoma, although less pronounced (fig. 26; see character 59).

Eriopterinae (figs. 12, 13, 15, 16, 26, 33), Hexatominae (figs. 58, 59) and Pediciini (figs. 94, 97) have the hypostoma divided, in Pediciini with a very characteristic push-button connection (fig. 97), in a few Eriopterinae with a hyaline connec-

tion between the anterior ends (*Rhabdomastix afra* (Wood 1952), *Gnophomyia jacobsoni* (fig. 16, Rogers 1927b) and probably also *Eugnophomyia luctuosa* (Rogers 1928)). In the lower hexatomine genera *Pseudolimmophila* (fig. 58) and *Paradelphomyia* (fig. 59), two, large, separated hypostomal plates are present. These are the only two genera of Hexatominae with a more or less compact head capsule. The other Hexatominae have the head capsule and the hypostoma reduced further with the ventral rods of the head capsule (which are homologous to the ventral inner margins of the genae) more widely separated (figs. 67, 68).

In *Ula* and the genera of the *Dactylolabis*-Tipulidae lineage the hypostoma is complete, although it is usually only narrowly continuous anteriorly and has a distinct posterior cleft (e. g. fig. 124). In *Pseudolimmophila*, *Paradelphomyia*, *Ula* and a number of genera of the *Dactylolabis*-Tipulidae lineage the hypostoma consists of two parts, namely a central part situated more ventrally and a lateral part situated more dorsally (figs. 59, 124, 131). The central part is apparently of labial and the lateral part of genal origin (see character 23 for details about the origin of the hypostoma).

Outgroup comparison reveals that the hypostoma consisting of a central and lateral part most probably represents a synapomorphy for Tipuloidea. Third level outgroups do not possess a hypostoma. In *Trichocera* and some second level outgroups (Anisopodidae: *Sylvicola*, *Mycetobia*) a hypostoma is not present but the ventral margins of the genae are connected by a posteriorly situated hypostomal bridge. Other second level outgroups (Psychodidae, Perissommatidae, Anisopodidae: *Olbiogaster*) as well as a few other families of Nematocera (Ptychopteridae, Culicidae, Simuliidae, Chironomidae) do possess a complete hypostoma. In these outgroups the hypostoma apparently does not show a subdivision in central and lateral parts (Anthon 1943a, 1943b, Harbach & Knight 1980, Teskey 1981, Peterson 1981). The posterior cleft is very rare among other Nematocera and might as well be considered a synapomorphy (a somewhat similar situation is found in the psychodid species *Philosepedon humeralis* (Meigen), Anthon 1943a: fig. 17, and the simuliid species *Metacnephia saileri* (Stone), Peterson 1981: fig. 86).

In Tipuloidea reduction of the hypostoma seems to be linked with reduction of the head capsule. Tipuloidea without a hypostoma possess a reduced head capsule, whereas first and second level outgroup taxa without a hypostoma do possess a compact head capsule. Therefore, an anteriorly toothed hypostoma as found in Tipuloidea with a compact

head capsule must be considered the groundplan condition of Tipuloidea. It is not yet clear whether the groundplan hypostoma is divided, as in lower Hexatominae (figs. 58, 59), or is complete as in all other Tipuloidea with a compact head capsule, except Pediciini. A transformation series from a complete hypostoma could include the following steps: in the first instance the posterior cleft evolved as a continuation of the anterior extension of the occipital foramen (character C), subsequently dividing the hypostoma, as in Pediciini, lower Hexatominae and lower Eriopterinae, with loss of the anterior teeth in higher Eriopterinae and higher Hexatominae.

The above transformation series together with the monophyly of the Pediciinae presumes that the divided hypostoma of Pediciini is an independent development. In most Pediciini the two hypostomal plates bear three apical teeth. These plates can be considered homologous to the lateral part of the hypostoma of *Ula* consisting also of three teeth in all species of which larvae are known. It must be concluded that in Pediciini the central labial part of the hypostoma is not present and was replaced by the push-button connection to keep the two lateral parts together.

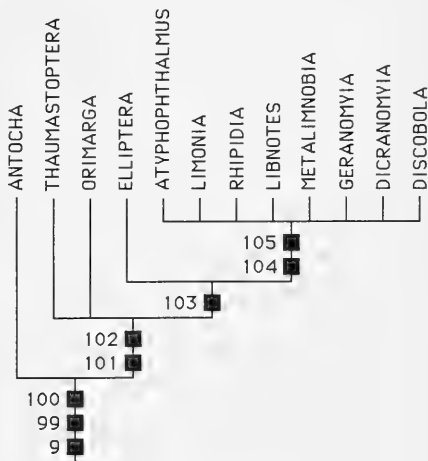


Fig. 8. Phylogeny of the Limoniinae.

Characters of the major groups

1. Margins of the externo- and interno-lateralia heavily sclerotized
2. Frontoclypeal apotome reduced (figs. 14, 19)
3. Genae with deep incisions (figs. 14, 21, 26, 33)

Head capsules of the Eriopterinae and Hexatominae are characterized by the above characters, to be considered derived in comparison with the more primitive head, as in the genera *Ula* to *Helius* of

figure 4. A posteriorly rectangular head capsule is present in *Pseudolimnophila* (fig. 58), *Cryptolabis* (Hynes 1963: fig. 3), *Cladura* (fig. 26) and *Chionea* (fig. 21), and might belong to the groundplan condition of the Eriopterinae-Hexamominae lineage. Further reduction of the head capsule in both subfamilies involves reduction of the amount of sclerotization of the area between the heavily sclerotized margins, resulting in the so-called dissected type of head, consisting mainly of elongate rods (e. g. figs. 13, 68, 69; see also characters 49, 67, and Crisp & Lloyd 1954: p. 280-281, Lindner 1959: p. 223-230).

4. Spiracles of the pupae not protuberant

In the first and second level outgroups, and in a number of other Nematocera, the lateral abdominal spiracles of the pupae are protuberant. This character is present in a number of Eriopterinae (Alexander 1920: *Erioptera*, *Ormosia*, *Symplecta*, *Gonomyia*, *Scleroprocta*; Byers 1974: *Idiogonomyia*) and Hexatominae (Alexander 1920: *Pseudolimnophila*; Wood 1952: *Conosia*), but not in the other Tipuloidea, except *Dactylolabis*. It is not clear whether the pupal spiracles are always protuberant in Hexatominae and Eriopterinae, but information about this character is not available for the majority of the taxa belonging to these two subfamilies.

5. Ventral anterior margins of genae slightly oblique or straight

In the first and second level outgroups, but also in the majority of the other families of Nematocera and in Nannochoristidae the ventral anterior margins of the genae which border the maxillae have a distinct oblique orientation, as in Eriopterinae (fig. 15) and Hexatominae (fig. 58). In all other Tipuloidea the orientation of these margins is slightly oblique (fig. 111) or straight (e. g. fig. 94). In Mecoptera (Nannochoristidae excluded), the ventral part of the head capsule is largely closed and difficult to compare but the ventral margins of the genae which border the maxilla are straight in *Panorpa* (Steiner 1930).

6. Prementum with protruding lateral corners

In Pediciinae the prementum is not rounded anteriorly as in other Tipuloidea (character 16), but appears as a flattened plate with protruding lateral lobes and is apically set with hairs (*Ula*) or spatulate setae (Pediciini, fig. 103). The prementum of Pediciinae is not very similar to the prementum in the first, second and third level outgroups which frequently possess a twofold or bilobed prementum (Steiner 1930, Anthon 1943a). It is nevertheless possible to consider the somewhat bilobed prementum of Pediciinae as symplesiomorphous with

respect to the anteriorly rounded prementum of the other Tipuloidea (character 16).

7. Larval antenna with two distinct papillae

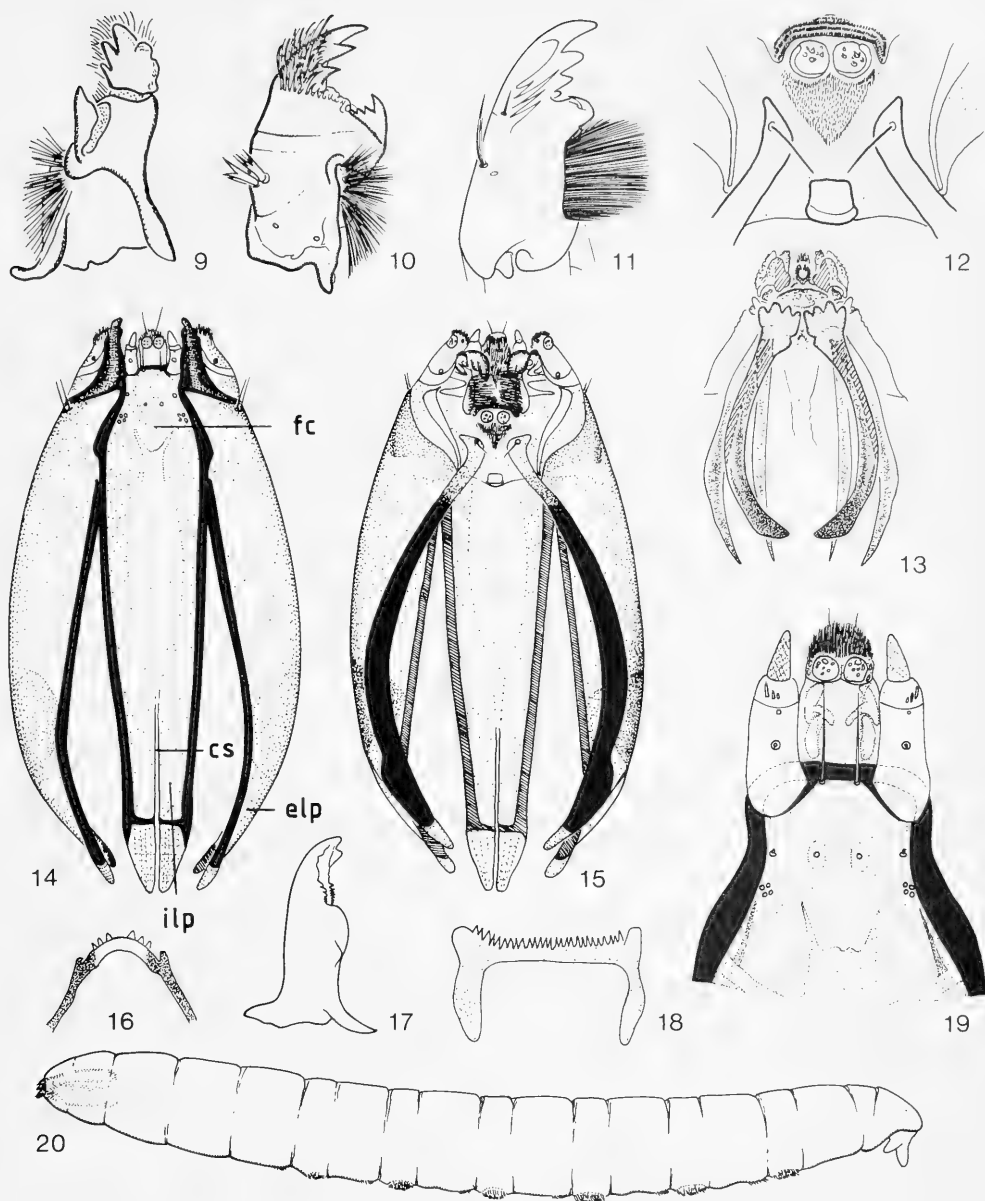
In the first and second level outgroups the larval antenna is usually very short. In Tipuloidea the antenna is usually elongated with a well developed basal segment, apically provided with small sensilla, a few hairs, and one distinct papilla (e. g. figs. 19, 26, 76). Relatively short antennae are found in *Ula* (fig. 114) and some *Dactylolabis* species. In most Pediciini and *Ula* the basal segment of the antenna bears two distinct papillae (figs. 98, 99, 114). This synapomorphy must be considered weak. One papilla is present in *Trichocera* and most second and third level outgroups but two papillae are present in some Anisopodidae (Keilin & Tate 1940, Anthon 1943a). According to Alexander (1920), two papillae are also present in *Pseudolimnophila* but this apparently applies to *P. inornata* only (Alexander 1920: fig. 174) and not to *P. luteipennis* (Malloch 1917) and *P. lucorum* (fig. 76; Brindle 1960, Rozkosny & Pokorný 1980). Furthermore, the character is lacking in some Pediciinae (see character 97).

8. Posterior incisions of genae narrow or hardly developed

Pediciini show the most massive head capsule. It is elongate without distinctly recognizable sutures and the posterior incisions of the genae are hardly developed (figs. 93, 94). A similar type of elongate head is present in *Ula mollissima* but with distinct frontal sutures (fig. 110). The absence of clearly developed posterior incisions of the genae in these taxa could be interpreted as a symplesiomorphy. However, a trend towards reduction of the posterior incisions is seen in other species of *Ula*, such as *U. sylvatica* and *U. elegans*, where the posterior incisions of the genae are well developed but narrow (fig. 116). Distinct posterior incisions are present in the younger larvae of *Ula* and Pediciini as well (figs. 95, 96; see also Lindner 1959).

9. Pupae in a silken cocoon

Larvae of Pediciini, *Ula* and Limoniinae construct a silken cocoon for the pupae. Among other Nematocera this character seems to be present only in Mycetophilidae (s.l.) and Simuliidae. On the basis of the adopted phylogeny it must be concluded that this character developed independently in Pediciinae and Limoniinae. Information about this character is not available for the limoniine genera *Libnotes* and *Discobola* (see also character 34). Larvae of the pediciine genus *Dicranota* living in lotic water apparently do not construct the pupal tubes unless they have some means of reaching the



Figs. 9-10. *Trichocera* spec., left mandible: 9, ventral view; 10, lateral view. – Figs. 11-20. Eriopterinae, larval characters. – 11, *Rhypholophus haemorrhoidalis*, left mandible, lateral view; 12, idem, labial region, ventral view; 13, *Molophilus* spec., head capsule, ventral view; 14, *R. haemorrhoidalis*, head capsule (fc, frontoclypeal apotome; cs, coronal suture; ilp, elp, interno- and externo-lateral parts of genae), dorsal view; 15, idem, ventral view; 16, *Gnophomyia jacobsoni*, anterior ends of ventral bars with hyaline connection; 17, *Cladura flavoferruginea*, left mandible, lateral view; 18, *Cheilotrichia cinerascens*, hypopharyngeal bar; 19, *R. haemorrhoidalis*, anterior part of head capsule, dorsal view; 20, *Chionea stoneana*, larva (probably third instar), lateral view (figs. 9-10: Anthon 1943a; 11, 12, 14, 15, 19: Lindner 1959; 13: Alexander & Byers 1981; 16: Rogers 1927b; 17: Alexander 1922; 18: Reusch 1988; 20: Byers 1983) (all figures redrawn).

banks of the river or stream, so that occasional pupae may be found free (Brindle 1967).

10. Mandibles operating in a horizontal plane

In the first and second level outgroups the mandibles have an oblique or vertical orientation, as in Eriopterinae, Hexatominiae and *Ula* (Perris 1847, Alexander 1915a, own observation). The mandibles of Pediciini have a slightly oblique orientation while feeding (Wardle 1926), but apparently move in a much more vertical direction when used as an aid in moving forward (Wardle & Taylor 1926). Propulsion aided by the mandibles is also known for *Ula* (Perris 1847, Alexander 1915a, 1920).

In the other Tipuloidea the mandibles operate horizontally, except in Cylindrotominae where they move vertical in second stage to full-grown larva, but horizontal in first stage larva (Bengtsson 1897, Alexander 1920, Peus 1952). Such a shift in the orientation of the mandibles is not known for other Tipuloidea and, for example, Byers (1983) recorded an oblique orientation in first instar to full grown larvae of *Chionea* (Eriopterinae).

11. Five-toothed hypostoma

In *Austrolimnophila*, *Epiphragma*, *Dicranoptycha*, *Lipsothrix* and first stage larvae of Tipulidae, the hypostoma is strikingly similar, consisting of three large central teeth in front and one small lateral tooth on either side situated more dorsally (figs. 124, 131). A five-toothed hypostoma is also present in *Helius* (fig. 135), *Limnophilomyia* and *Elephantomyia aurantiaca* (fig. 170). The presence of a five-toothed hypostoma in this wide range of taxa indicates that this is the basic number of hypostomal teeth for part of the Tipuloidea with a complete hypostoma.

A higher number of teeth is found in Eriopterinae (*Molophilus* 8, *Erioptera* 10), Hexatominiae (*Paradelphomyia* 8-10, *Pseudolimnophila* 14-16), Pediciinae (Pediciini 6-8, *Ula* 9), *Dactylolabis* (9-11), *Atarba* (7), Limoniinae (usually 9-11, in *Dicranomyia*, *Libnotes* and *Metalimnobia* up to 17), Cylindrotominae (about 15) and Tipulidae (full grown larvae 7-9)¹.

12. Maxillary palpus

The maxillary palpus in first and second level outgroups is flush with the surface of the maxilla, recognizable only by a ring of chitin surrounding the sensilla (chapter 3: character 45). This type of maxillary palpus is found in Eriopterinae (fig. 23), Hexatominiae, Pediciini (the two last-mentioned taxa with the outer maxillary lobe elongate and the sensilla situated near or at the apex, figs. 68, 100), *Ula* (fig. 113) and *Dactylolabis*. In other Tipuloidea the sclerotized ring surrounding the sensilla is cy-

lindrical and usually well developed (figs. 121, 151, 163, 178), but with a low profile in *Helius* (fig. 133) and several species of Limoniinae (fig. 152).

13. Labral sclerites

The genera *Austrolimnophila* and *Epiphragma* share a number of larval and pupal characters, such as shape of the mandible, antenna, maxilla, hypopharynx, armature of pupal abdominal segments (Alexander 1920, Bruch 1939, Wood 1952, Lindner 1959, Brindle 1960). A distinct synapomorphy for both genera is the peculiar shape of the labral sclerites (figs. 126, 129).

14. Pupal armature

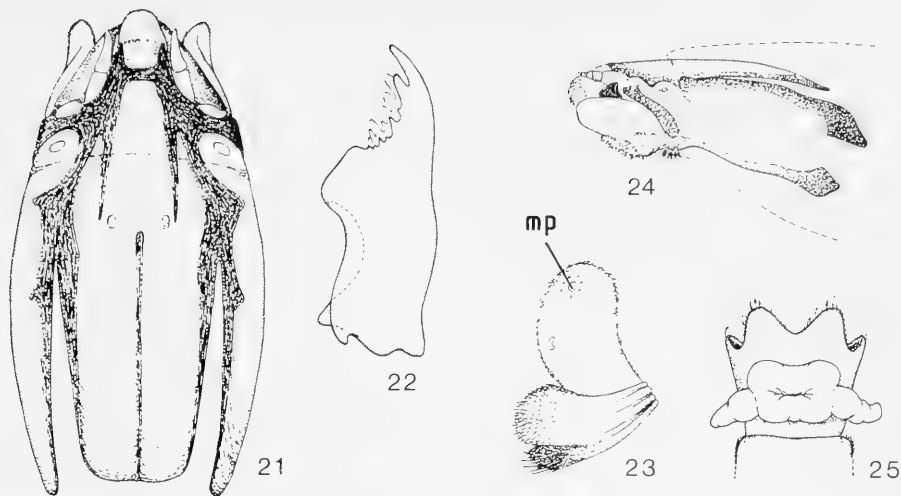
One or more rows of spines are usually present along the posterior margin of the pupal abdominal segments in Tipuloidea (e. g. fig. 47) and a great deal of other Nematocera (Brauns 1954b). Such rows are absent in lower Eriopterinae (character 53), *Dicranoptycha*, *Helius*, *Lipsothrix*, *Limnophilomyia* (fig. 153), Limoniinae (fig. 157-159; *Discobola caesarea* excepted?, see Mik 1884), and Cylindrotominae (fig. 156), but are present in Tipulidae. In Hexatominiae the spines can be distinctly tubular (character 75).

15. Hypopharynx dentated

16. Prementum dentated

Below the ventral floor of the pharynx, most taxa of the *Helius*-Tipulidae lineage are provided with three rows of teeth, namely the hypopharynx, prementum and hypostoma (fig. 149). The hypopharynx of Tipuloidea and first and second level outgroups (Anthon 1943a), is usually preserved as a hemispherical cushion or lobe, densely set with setae or minor prominences and supported by a U- or H-shaped, sclerotized bar (figs. 122, 132, 175, 176). Deviations from this groundplan condition are: higher Hexatominiae: sclerotized bar transformed into the very typical hypopharyngeal skeleton (character 67). Pediciini: central part of bar not sclerotized (Reusch 1988: fig. 38B). *Ula*: hypopharynx incorporated in the pharyngeal filter apparatus (details in Lindner 1959). *Helius*, *Limnophilomyia*, Limoniinae and Cylindrotominae (character 15): hypopharynx not hemispherical but sclerotized and distinctly dentated (figs. 147,

¹ Five teeth is mentioned for *Longurio minusculus* Alexander (Wood 1952), and *Tipula (Trichotipula) oropetoides* Johnson (Alexander 1920). In both instances the prementum has three teeth. In Tipulidae the prementum of the first stage larvae has three teeth and that of the full grown larvae five teeth. Three premental teeth in the above two species might indicate that the described larvae were not full grown.



Figs. 21-25. Eriopterinae, larval characters. – 21, *Chionea stoneana*, head capsule, dorsal view; 22, idem, left mandible, ventrolateral view; 23, idem, left maxilla (mp, maxillary palp), ventral view; 24, *Idiognophomyia enniki*, head capsule, lateral view; 25, idem, terminal segment, ventral view (figs. 21-23: Byers 1983; 24, 25: Byers 1974) (all figures redrawn).

148, 167, 168). This synapomorphy must be considered weak because it is absent in *Lipsothrix* (Rogers & Byers 1956, Hynes 1965) and Tipulidae (fig. 176).

The prementum of Tipuloidea is usually hardly sclerotized and anteriorly rounded, the ventral surface provided with hairs, bristles or spines (fig. 122), and bearing the rudimentary labial papillae (figs. 122, 148). In lower Hexatomiinae (*Pseudolimnophila*) the outer margin is set with minor teeth. In Pediciinae the prementum has the outer lobes produced (fig. 103; character 6). A sclerotized and distinctly dentated prementum (character 16) is present in the taxa of the *Helius*-Tipulidae lineage (figs. 147, 148, 167, 168, 175, 176), *Limnophilomyia* excepted (Wood 1952). Limited information is available for *Lipsothrix* and *Limnophilomyia* but the prementum is very similar in *Helius*, Limoniinae and Tipulidae, with the orifice of the salivary duct between prementum and hypopharynx. In Cyndrotomiinae the orifice is situated more in front, just below the outer row of teeth (figs. 167, 168), indicating that this row of teeth might not belong to the prementum but to the hypopharynx.

17. Interno-lateralial fused with frontoclypeal apotome

In *Lipsothrix*, *Limnophilomyia*, Limoniinae, Cyndrotomiinae and Tipulidae the internal lateral parts of the genae are fused with the frontoclypeal apotome (fig. 140). In all other Tipuloidea with a

complete hypostoma the interno-lateralial and the frontoclypeal apotome are separated by the frontal sutures (fig. 134).

18. Inner maxillary lobe with a separate sclerotized plate

A separate sclerotized plate on the inner maxillary lobe between the cardo and the sclerotization along the outer margin of the lobe is present in Limoniinae, Cyndrotomiinae and Tipulidae (figs. 151, 152, 163, 173, 178) and not in other Tipuloidea (figs. 100, 113, 121). It is not known whether this character occurs in *Lipsothrix* and *Limnophilomyia*, and whether one of the sclerotized plates on the inner maxillary lobe in *Helius* (fig. 133) represents the same plate.

19. Externo-lateralial strengthened

In Limoniinae, Cyndrotomiinae and Tipulidae the externo-lateralial are strengthened by distinct sclerotizations bordering the genae in front of the area of the growth lines (figs. 139, 140, 160, 173). It is not known whether this character is present in *Lipsothrix* and *Limnophilomyia*.

20. Spiracular field with two dorsal lobes

Two dorsal lobes in addition to the dorso-lateral and ventro-lateral lobes of the spiracular field are present in Tipulidae and Cyndrotomiinae only (figs. 164, 177). This synapomorphy is considered weak because it is not clear whether the dorsal lobes in Cyndrotomiinae do in fact represent ab-

dominal lobes. Furthermore, absence of these lobes in species of *Cylindrotoma* could represent the groundplan condition in Cylindrotominae.

21. Premaxillary suture and side plates

In Tipulidae and Cylindrotominae distinct side plates are found (Peus 1952: 'Seitenplatten'), separated from the ventral and lateral parts of the head capsule by a premaxillary suture sensu Cook (1949) (figs. 160, 173). In both families the side plates include the stemmata (Cook 1949, Peus 1952). In the other Tipuloidea the side plates and premaxillary suture are absent.

22. Prostheca on a separate sclerite

A prostheca in the form of a brush of long hairs arising directly from the surface the mandible is found in all Nematocera (figs. 9-11). As far as is known only in full grown larvae of Tipulidae and Cylindrotominae the prosthecal brush is situated on a separate sclerotized lobe (figs. 162, 179, 180; see also chapter 3, Tipuloidea and 'all other Nematocera' as sistergroups).

23. Hypostoma of first stage larvae different

As outlined above, the presence of an anteriorly toothed hypostoma is considered to belong to the groundplan condition in Tipuloidea (character G). Several authors are of the opinion that the hypostoma is of genal origin (e.g. Anthon 1943a, 1943b, Snodgrass 1960, Matsuda 1965), whereas others claim a labial origin (e.g. de Meijere 1917, Cook 1949, Saether 1971, see also Hennig 1973, Teskey 1981). The third alternative of a combined genal and labial origin, postulated by Bengtsson (1897) and again by Courtney (1990, 1991), is demonstrated in Cylindrotominae and Tipulidae (and might belong to the groundplan condition in Tipuloidea with a complete hypostoma or even all Tipuloidea), where the anterior part, the true hypostoma, is of labial origin and the posterior part, the hypostomal or subgenal bridge, is of genal origin.

In Tipulidae and Cylindrotominae there are marked differences between the hypostoma of the first stage larvae and the full grown larvae, whereas in other Tipuloidea the hypostoma of the first stage larvae and the full grown larvae seem in principal to be the same. The latter statement, however, is based on limited information. Available for examination were first stage larvae of Cylindrotominae (*Diogma*, *Phalacrocer*), Tipulidae, Limoniinae, (*Limonia*, *Metalimnobia*, *Dicranomyia*), *Helius*, *Austrolimnophila* (*Limnophilella*), *Hexatoma* and *Erioptera*. Published accounts on the hypostoma of first stage larvae do hardly exist. To be mentioned are Bengtsson (1897, Cylindrotominae: *Phalacrocer replicata*), Crisp & Lloyd

(1954, Tipulidae), and Okely (1979, Pediciinae: *Tricyphona immaculata*; Eriopterinae: *Erioconopa trivialis*).

The hypostoma in first stage larvae of Tipulidae appears as a large, 5-toothed plate (see character 11). This plate lies in isolation behind the two sclerotized plates which represent the side plates. The isolation of the hypostoma from the genae indicates that it is of labial origin. In the full grown larvae of Tipulidae the general appearance of the hypostoma is the same as in the other Tipuloidea with a complete undivided hypostoma, and has become a 7- or 9-toothed plate, fused with the inner ventral margins of the genae (fig. 173).

First stage larvae of Cylindrotominae (*Diogma*, *Phalacrocer*) (fig. 165) possess a complete subgenal bridge which is maintained in the full grown larvae. Its presence can be considered plesiomorphic (Teskey 1981), but in other Nematocera this bridge is formed by the posterior margin of the genae, whereas in Cylindrotominae it is formed anteriorly and homologous with the side plates. Situated in front of and slightly above this heavily sclerotized bridge, the first stage larvae possesses a small, completely hyaline, bilobed plate, the hypostoma. Its position and the difference in sclerotization indicate that this small plate is of labial origin, as was pointed out already by Bengtsson (1897). In full grown larvae of Cylindrotominae the hypostoma has become a distinct, sclerotized and multidentated plate, completely fused with the subgenal bridge, but with distinct lines of fusion (fig. 166).

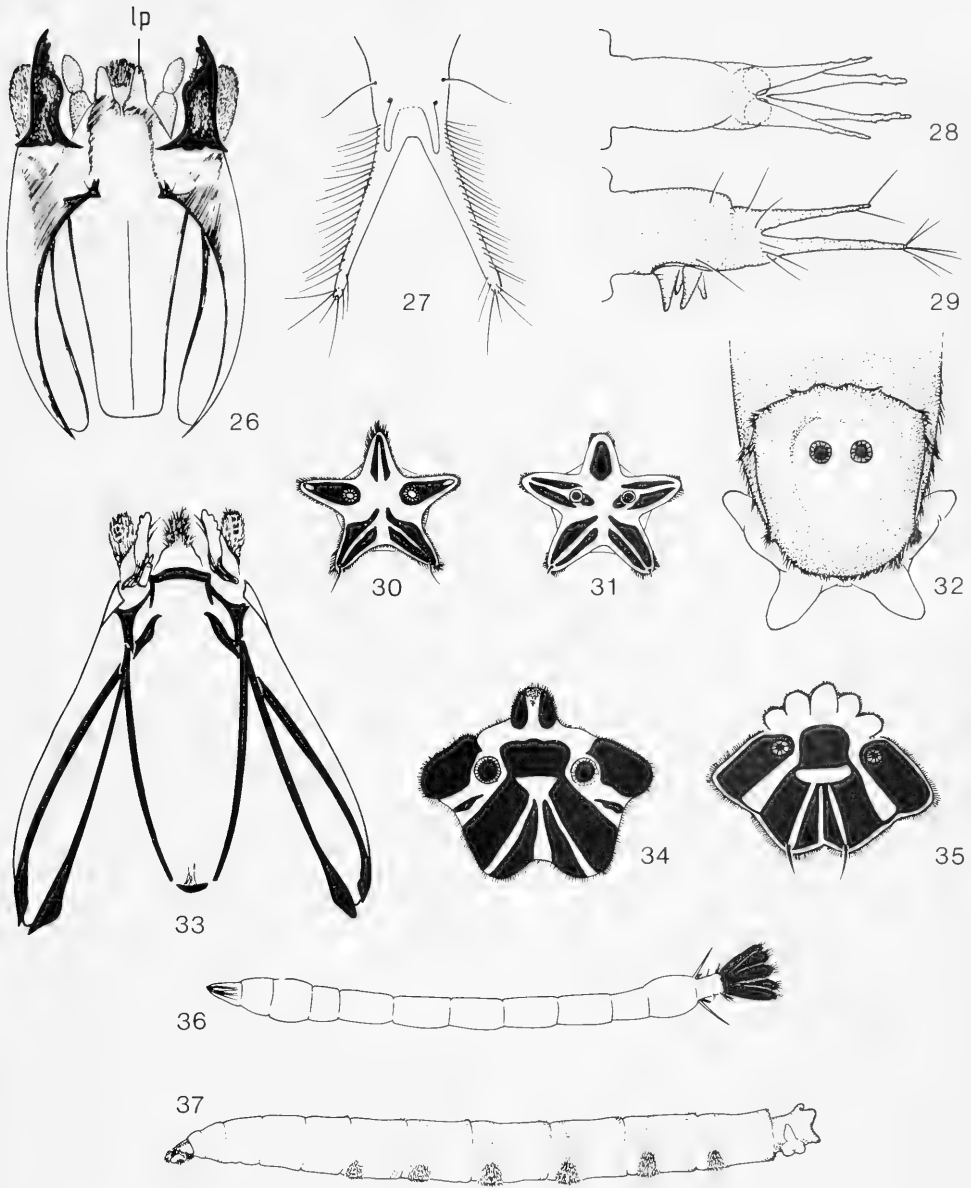
As far as is known, the hypostoma of the first stage larvae of the other Tipuloidea does not show the developments found in Tipulidae and Cylindrotominae. In the first stage larvae of the other Tipuloidea the hypostoma already possesses the same number of teeth as found in the full grown larvae, and it is fused with the ventral margins of the genae. In several genera a distinct line is visible at the transition of the genae and the hypostoma, apparently representing the line of fusion. It must be concluded that in the other Tipuloidea fusion of genae and hypostoma already occurs in the egg.

24. Head capsule elongate

In comparison to Mecoptera, Nematocera and other Tipuloidea (e. g. fig. 119), the Eriopterinae, Hexatominae and Pediciinae possess an elongated head capsule, about twice as long as broad (e. g. figs. 14, 66, 93). These elongate head capsules are characterized by the very narrow coronal suture.

25. Interno-lateralial extended dorsally

In larvae of Eriopterinae, Hexatominae and Pediciinae the interno-lateralial of the genae occupy



Figs. 26-37. Eriopterinae, larval characters. – 26, *Cladura flavoferruginea*, head capsule (lp, labral papilla), ventral view; 27, *Baeoura claripennis*, terminal segment, dorsal view; 28, *Cryptolabis magnistyla*, terminal segment, dorsal view; 29, idem, lateral view; 30, *Cheilotrichia cinerascens*, spiracular disc; 31, *Molophilus* spec., spiracular disc; 32, *Chionea stoneana*, terminal segment, posterodorsal view; 33, *Gonomyia sulphurelloides*, head capsule, dorsal view; 34, *Eugnophomyia luctuosa*, spiracular disc; 35, *Ellipteroides lateralis*, spiracular disc; 36, *Scleroprocta* spec., larva, dorsal view; 37, *Idiognophomyia enniki*, larva, lateral view (fig. 26: Alexander 1922; 27, 33: Wood 1952; 28, 29: Hynes 1963; 30, 31: Lindner 1959; 32: Byers 1983; 34: Rogers 1928; 35: Bangerter 1928; 36: Alexander 1920; 37: Byers 1974) (all figures redrawn).

most of the dorsal part of the head capsule and the frontoclypeal apotome is reduced (fig. 14) or entirely fused with the interno-lateralis (fig. 93).

26. Penultimate segment inflated

Larvae of Eriopterinae, Hexatominæ and Pediciini are able to inflate the penultimate segment (fig. 64). This character, not known from first to third level outgroups or other Tipuloidea except *Atarba picticornis* (Rogers 1927a), is widespread in all three taxa but is not recorded for all genera, most probably because it is not a permanent, structural character. Inflation is observed most frequently in moving animals and is achieved within a few seconds, apparently to afford anchorage to the substrate (Crisp & Lloyd 1954, Lindner 1959).

27. Outer maxillary lobe lengthened

The maxillary lobes of Tipuloidea larvae are usually short (e. g. figs. 23, 121) as in other Nematocera, whereas in Hexatominæ, Pediciini and some Eriopterinae (*Cryptolabis* and *Rhabdomastix*) the outer maxillary lobe is lengthened (figs. 58, 60, 66-69, 100). Lengthened maxillae are usually considered to be correlated with the predatory feeding of Hexatominæ and Pediciini but they are also present in the less- or non-predatory genera *Paradelphomyia*, *Pseudolimnophila*, *Neolimnomyia*, *Cryptolabis* and *Rhabdomastix*. The presence of lengthened maxilla in especially the two last-mentioned and apparently not closely related genera indicates, that this character evolved independently in Eriopterinae and perhaps also in Hexatominæ and Pediciini.

The outer maxillary lobe of *Pseudolimnophila* (fig. 58) with two joints, each with a ring sclerite, very much resembles that of Mecoptera (Steiner 1930), including Nannochoristidae (Pilgrim 1972), but in *Pseudolimnophila* the inner lobe is not distinctly separated from the outer lobe (Crisp & Lloyd 1954).

28. Spiracles on dorsum of pupal tergite 8

Nematocera pupae apparently do not possess spiracles on the dorsum of tergite 8. An account of such spiracles was found only for the Pachyneuridae (Krivosheina & Mamaev 1970). In Tipuloidea spiracles on the dorsum of tergite 8 are in general absent in Eriopterinae, Hexatominæ, *Dactylolabis* and *Dicranoptycha*, but are present in most of the other groups except Cylindrotominae and Tipulidae, of which the pupae are propneustic although some lower Tipulidae do possess spiracles on the dorsum of tergite 8 (Wood 1952). It is not known whether this character occurs in *Limnophilomyia*, *Lipsothrix*, and several Limoniinae (*Discobola*, *Geranomyia*, *Rhipidia*). In Hexatominæ these spiracles

are present in *Paradelphomyia senilis* (Reusch 1988), *Euphyllidorea meigeni* (own observation) and they are figured by Wiedenska (1987) for *Phyllidorea nigronotata* but are absent in the other *Phyllidorea* species studied by her. In Limoniinae they are absent in *Antocha* and *Elliptera* (own observation).

29. Larvae without ventral creeping welts

Presence of ventral creeping welts, densely set with recurved hooklets or spinules, can be considered plesiomorphic. Such welts are found in larvae of many Nematocera and Tipuloidea. In Tipuloidea they are in general present on the anterior part of segments 5-10 (e. g. figs. 37, 109). Some Limoniinae possess additional creeping welts on segments 2-4 and 10 (figs. 143, 144). In *Trichocera* ventral creeping welts are not present. In Eriopterinae and Hexatominæ presence of ventral creeping welts, again on sternites 5-10, is restricted to a few genera (characters 48, 79). In the Pediciini ventral creeping welts are restricted to sternites 6-10 or 7-10 (figs. 107, 108), with the welts developed into pseudopods in certain genera (fig. 104; characters 84, 91, 95). Several species of *Epiphragma* and certain subgenera of *Tipula* (Gelhaus 1986: *Arctotipula*, *Nippotipula*, *Sinotipula*) have naked transverse swellings which lack recurved hooklets or spinules. Ventral creeping welts are absent in *Dactylolabis* and Cylindrotominae.

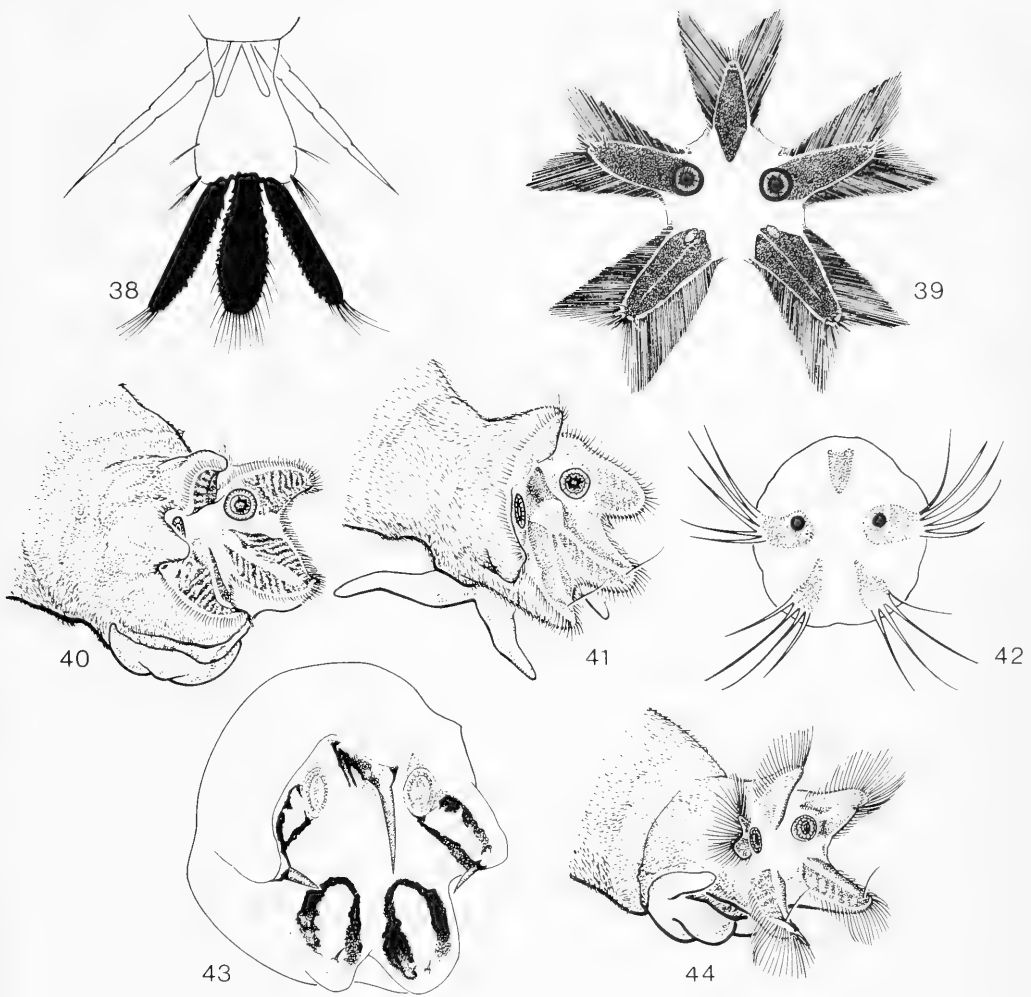
30. Larvae with dorsal creeping welts

Presence of dorsal creeping welts can be considered derived because Nematocera larvae rarely possess dorsal creeping welts (in contrast to Brachycera). Dorsal creeping welts occur frequently again on the anterior part of segments 5-10, with additional welts in certain Limoniinae. In *Trichocera* dorsal welts are absent. Among the higher Hexatominæ dorsal creeping welts on tergites 5-10 are restricted to a few genera (character 79). Dorsal creeping welts in Pediciini are known for *Rhaphidolabina flaveola* only (Alexander 1920). A very special arrangement of convergent dorsal welts is found in a number of species of *Dactylolabis* (Nowicki 1867, Bangerter 1931, Sinclair 1988). In Tipulidae naked transverse dorsal swellings are present in *Tipula* (*Nippotipula*) (Gelhaus 1986).

31. Pupae with ventral creeping welts

32. Pupae with dorsal creeping welts

Pupae of Tipuloidea frequently possess dorsal and/or ventral creeping welts on the abdominal segments (figs. 153, 154, 157). It is not certain whether presence of these welts should be considered derived, but welts seem to be rare in pupae



Figs. 38-44. Eriopterinae, larval characters. – 38, *Scleroprocta* spec., terminal segment, ventral view; 39, *Rhypholophus haemorrhoidalis*, spiracular disc; 40, *Gnophomyia toschiae*, terminal segment, oblique posterior view; 41, *Gonomyia* spec., terminal segment, oblique posterior view; 42, *Eriocnopa trivialis*, spiracular disc of first instar; 43, *Rhabdomastix californiensis*, terminal segment, oblique posterior view; 44, *Ormosia* spec., terminal segment, oblique posterior view (fig. 38: Alexander 1920; 39: Lindner 1959; 40, 41, 44: Alexander & Byers 1981; 42: Okely 1979; 43: Hynes 1969c) (all figures redrawn).

of other Nematocera (Brauns 1954b). In pupae of *Trichocera* welts are absent. In pupae of Tipuloidea the welts usually occur on abdominal tergites 3-7 and sternites 5-7. In the Eriopterinae dorsal and ventral welts are present in the pupae of *Gnophomyia*, *Idiognophomyia*, *Hesperoconopa*, and some species of *Gonomyia*. The creeping welts in pupae of Pediciini are discussed under character 96.

33. Pupae with inner legsheaths the longest

In Mecoptera including Nannochoristidae and the majority of the Nematocera and Tipuloidea, the outer legsheaths of the pupae are the longest (fig. 154) although in Eriopterinae, Hexatominae, *Epiphragma*, *Ula* and *Cylindrotominae*, some species or specimens do possess leg sheaths of equal length. In *Dactylolabis*, *Helius*, *Limnophilomyia* and Limoniinae the inner legsheaths are usually the longest but also in these taxa, species or specimens might show equal leg sheaths. Mik (1886) figured outer leg sheaths the longest in *Elliptera*, but pupae of this genus examined had equal leg sheaths. The special arrangement of the leg sheaths in Eriopterinae is discussed under character 37.

34. Larvae with spinning glands

The larvae of a number of species possess spinning glands. Except for *Cylindrotoma*, the larva of the species concerned constructs a case or a cocoon in which pupation takes place. In *Dicranoptycha* and the limoniine genus *Thaumastoptera* a case is constructed out of small pieces of wood, leaves or fine grains of sand. All species with spinning glands, except *Dicranoptycha*, possess real silk glands to produce a silken cocoon covered with detritus for pupation or, in *Thaumastoptera*, to produce a silken inner lining to their cases. Many larvae of Limoniinae are living in silken tubes themselves as well (character 99). The only account for *Cylindrotominae* is by Cameron (1918) who reported for the terrestrial *Cylindrotoma splendens* [= *distinctissima americana*] that young larvae have the power 'of secreting a silken thread from the mouth, which is probably the product of the salivary glands. They frequently adhered to this thread ... used in transferring them from one leaf to another'.

35. Apophyses present

A number of Tipuloidea possess small sclerotized appendages posterior to the hypostoma (figs. 97, 135). They play part in the attachment of the prothoracic skin to the larval head capsule (Peus 1952), and are not present in other Nematocera or the related orders. Apophyses are not figured or described for *Dactylolabis* (Bangertner 1931,

Brindle 1960, Sinclair 1988), but in *Dactylolabis montana* they are present (own observation).

5. ERIOPTERINAE

Introduction

The monophyly of the Eriopterinae is based on two rather weak characters only (fig. 5). Larvae of Eriopterinae usually possess a narrow labrum (figs. 13, 19, 21, 26, 33), slender mandibles (figs. 11, 17, 22), simple maxillae (fig. 23) and relatively well developed antennae with a distinct, usually somewhat asymmetrical apical papilla (figs. 19, 21, 26). These characters are not listed as synapomorphies because they might as well represent the ground-plan condition in Tipuloidea.

The amount of information on the head capsule of *Baeoura* is limited, described by Wood (1952) for the species *claripennis* as follows: 'Head capsule long and slender, consisting of three concave plates, one dorsal and two lateral, the margins of which are heavily chitinized. Labrum and maxilla as in the genus *Gonomyia*. Remainder of head capsule difficult to distinguish and cannot be accurately described'.

Character 49, head capsule further reduced, is taken as landmark between the lower and higher Eriopterinae. The lower Eriopterinae include the Cladurini (the genera *Cryptolabis*, *Gladura* and *Chionea*). Character 39 suggests that this tribe can also be recognized on the basis of the larvae. Genera belonging to the Gonomyiini are found in one section of fig. 5 except *Gonomyodes*, partly as lower and partly as higher Eriopterinae. *Styringomyia*, placed in the Eriopterini by Hynes (1990) is found amidst the Gonomyiini. The tribes Eriopterini and Molophilini do not show a close correspondence to the phylogenetic arrangement presented.

Eriopterinae larvae are gross-feeding forms on decayed plant remains (Crisp & Lloyd 1954). Strictly predatory forms are not known, but according to Byers (1983), *Chionea* certainly is not a typical herbivorous tipuloid and might be carnivorous.

In the text below reference is made to characters of the genera included in fig. 5. Other eriopterine genera are mentioned in chapter 9.

Characters

36. Last larval segment constricted

In almost all Eriopterinae the last larval segment is basally constricted (figs. 36, 37) and can be telescoped into the penultimate segment during progression, a way of propulsion also recorded by

Alexander (1920) for *Ula*. No constriction is found in *Cladura* and *Chionea* (fig. 20). Information about this character is equivocal or not available for *Eugnophomyia*, *Arctocnopa*, *Erioconopa*, *Ilisia* and *Hoplolabis*. This synapomorphy must be considered weak because it is also found in a number of Hexatominæ (character 76).

37. Sheaths of middle legs the shortest

Pupae of Eriopterinae species frequently have the middle legsheaths the shortest (figs. 45, 52, 54), usually with the outer legsheaths the longest, but sometimes with the inner and outer legsheaths of equal length. This character is not present in other Tipuloidea except *Atarba* (see chapter 9) and apparently does not occur in other Nematocera. Therefore, it is listed here as a synapomorphy although it is not exhibited by all Eriopterinae. The character is present in *Cryptolabis*, *Cladura*, *Styringomyia ingrami* (Edwards 1924), *Eugnophomyia*, *Gonomyia*, *Ellipteroides*, *Cheilotrichia*, *Symplecta*, *Ormosia*, *Rhypholophus*, *Gonomyodes*, *Ilisia*, *Hoplolabis*, *Erioptera* and *Molophilus*. The legsheaths are of equal length in *Baeoura* (Wood 1952), some species of *Gnophomyia* (Malloch 1917), in *Styringomyia neocaledoniae* (Hynes 1990) and in *Scleroprocta* (Alexander 1920, Bangerter 1930, Brindle 1967). Outer legsheaths the longest and inner legsheaths the shortest is found in *Chionea* (Byers 1983), *Idiognophomyia* (Byers 1974), *Gnophomyia* (Alexander 1920; Rogers 1927b) and *Rhabdomastix* (Hynes 1969c). Information about this character is not available for *Arctocnopa* and *Erioconopa*.

38. Pupae without respiratory horns

Pupae of Tipuloidea usually possess respiratory horns, present also in all Eriopterinae included in fig. 5, except *Baeoura*, *Cryptolabis*, *Cladura*, and *Chionea*.

39. Labral papilla

Larvae of *Cryptolabis*, *Cladura* (fig. 26), and possibly also *Chionea* (fig. 21) possess 'two large cylindrical papillae which arise near the clypeo-labral suture and which appear to belong to the labrum' (Hynes 1963 for *Cryptolabis*), not present in other Tipuloidea or Nematocera.

40. Last larval segment not constricted

Synapomorphy 36 is not present in *Cladura* and *Chionea* (fig. 20).

41. Spiracular lobes absent

Cladura and *Chionea* (fig. 32) do not possess spiracular lobes (see also character 43).

42. Palpsheaths obliquely directed downward

In Psychodidae, Trichoceridae, Anisopodidae, Scatopsidae and most other families of Nematocera, the palpsheaths of the pupae are directed obliquely upward. This is also the case in the majority of the Tipuloidea with a compact head capsule. In Hexatominæ the maxillary palps are usually horizontal or apically curved downward (figs. 87-90). In *Phylidorea*, *Euphylidorea*, *Eleoephila* and *Hexatoma* horizontal as well as slightly upcurved sheaths are found. In Eriopterinae the sheaths of the palps are obliquely directed downward (e. g. fig. 47), except for *Baeoura* (upward), *Cryptolabis* (horizontal), *Chionea* (upward, fig. 46) and *Cladura* (upward).

43. Spiracular field with five more or less identical lobes

44. Darkened spots on ventral spiracular lobes divided into two

The apparent plesiomorphic condition of four spiracular lobes is present in *Baeoura* (fig. 27) and *Cryptolabis* (figs. 28, 29). In these two genera the lobes are rounded and without dark markings. Lobes are absent in *Cladura* and *Chionea* (character 41). The other Eriopterinae usually possess five more or less identical lobes with the dark markings on the ventral lobes divided into two (e. g. fig. 39). The number of spiracular lobes is seven in *Styringomyia* and *Gonomyodes*, and nine in *Ellipteroides* (fig. 35), while the genera *Rhabdomastix*, *Arctocnopa* and *Gonomyia* have shortened lobes.

Character 44 must be considered a weak synapomorphy, because it is also present in a number of Hexatominæ (character 80). It is not found in *Styringomyia*, *Gonomyodes* and some species of *Rhabdomastix* and *Symplecta* (see also characters 55, 61, 62).

45. Pupae with dorsal and ventral creeping welts

46. Respiratory horns earshaped

47. Posterior anal papillae longer than posterior ones

Idiognophomyia and *Gnophomyia* are considered sister genera on the basis of the above three characters although character 45 is found in *Gonomyia* as well, character 46 in some species of *Gonomyia* (fig. 48) and *Ellipteroides*, and character 47 (fig. 25) in *Scleroprocta*, *Ormosia* (fig. 44) and *Rhypholophus*.

48. Larvae with ventral creeping welts

As outlined above (character 29), larval creeping welts on sternites 5-10 is apparently plesiomorphic. This character is present in *Cladura*, *Chionea* (fig. 20), *Idiognophomyia* (fig. 37) and *Gnophomyia*. Loss of creeping welts can be considered a

synapomorphy for the higher Eriopterinae but occurred also in *Baeoura* and *Cryptolabis*. Ventral creeping welts are absent as well in the majority of Hexatomininae (character 79). Therefore, it appears more parsimonious to accept presence of ventral creeping welts as independent returns to the plesiomorphic condition in the *Chionea-Cladura* and *Idiognophomyia-Gnophomyia* lineages.

49. Head capsule further reduced

A still rather compact head capsule is found in the so-called lower Eriopterinae (figs. 21, 26). In the higher Eriopterinae the head capsule is reduced further. The amount of sclerotization between the heavily chitinized margins is minimized and the head capsule appears as consisting mainly of elongate, strongly sclerotized rods (figs. 13-15, 33). These rods are homologous to the heavily chitinized margins which border the frontoclypeal apotome and loop around the genae. A break in the loop around the genae is found already in *Idiognophomyia* and *Gnophomyia* (fig. 24).

50. Mesothorax of pupae with distinct crest

Pupae of higher Eriopterinae, *Styringomyia* and *Gonomyodes* excepted, possess a distinct crest on the mesothorax (figs. 47, 48, 50, 51). This crest is absent in other Tipuloidea, some South African species of *Limnophila* excepted (fig. 87; Wood 1952).

51. Larval antennae near to each other

In higher Eriopterinae, *Styringomyia* excepted, the larval antennae are situated very near to each other (fig. 19). This character is not found in other Tipuloidea except *Idiognophomyia*. No information is available for *Baeoura*, *Rhabdomastix* and *Gonomyodes*.

52. Central part of spiracular field with a distinct dark marking

Among Eriopterinae a distinct dark marking between the spiracles is present in *Eugnophomyia*, *Gonomyia* and *Ellipteroides* only (figs. 34, 35, 41).

53. Pupal abdominal spines

Distinct rows of spines (figs. 47, 49, 50) are usually present along the posterior margin of the abdominal segments of the higher Eriopterinae, except for *Styringomyia*, *Rhabdomastix*, *Eugnophomyia*, *Gonomyia* and *Ellipteroides*, whereas no information about this character is available for *Arctoconopa* and *Erioconopa*. Similar rows of spines are present in other Tipuloidea (character 14). Their absence in lower Eriopterinae might indicate that spines in higher Eriopterinae is a de novo development.

54. Larvae with statocysts

Statocysts, lateral sacs on the last abdominal segments of the larvae, have been observed in species of *Cheilotrichia*, *Symplecta*, *Ormosia*, *Rhypholophus*, *Ilisia*, *Erioptera* and *Molophilus* (Wolff 1922; Crisp & Lloyd 1954). Information for most other Eriopterinae is not available, but statocysts are apparently absent in *Chionea* (Byers 1983), *Gonomyia* (Crisp & Lloyd 1954) and all other Nematocera and Tipuloidea except for some higher Hexatomininae (Wolff 1922, Crisp & Lloyd 1954; character 68).

A detailed account of these organs is given by Wolff (1922), their functioning as statocysts is described by von Studnitz (1932). Statocysts control the geotactic reactions and are thought to be associated with larvae that swiftly move through the mud (Crisp & Lloyd 1954).

55. Hairs on spiracular lobes

In Eriopterinae with five or more spiracular lobes, the hairfringe around the spiracular field is usually continuous (figs. 30, 32, 34, 35, 40, 41). In the *Symplecta-Molophilus* lineage the hairfringe is interrupted and the hairs are concentrated on the spiracular lobes (figs. 31, 39, 44). This character must be considered weak because the original configuration of the hairfringe is not always maintained in preserved material, and likewise not always accurately described or illustrated. Furthermore, this character is apparently present in *Idiognophomyia* (Byers 1974) and some species of *Rhabdomastix*.

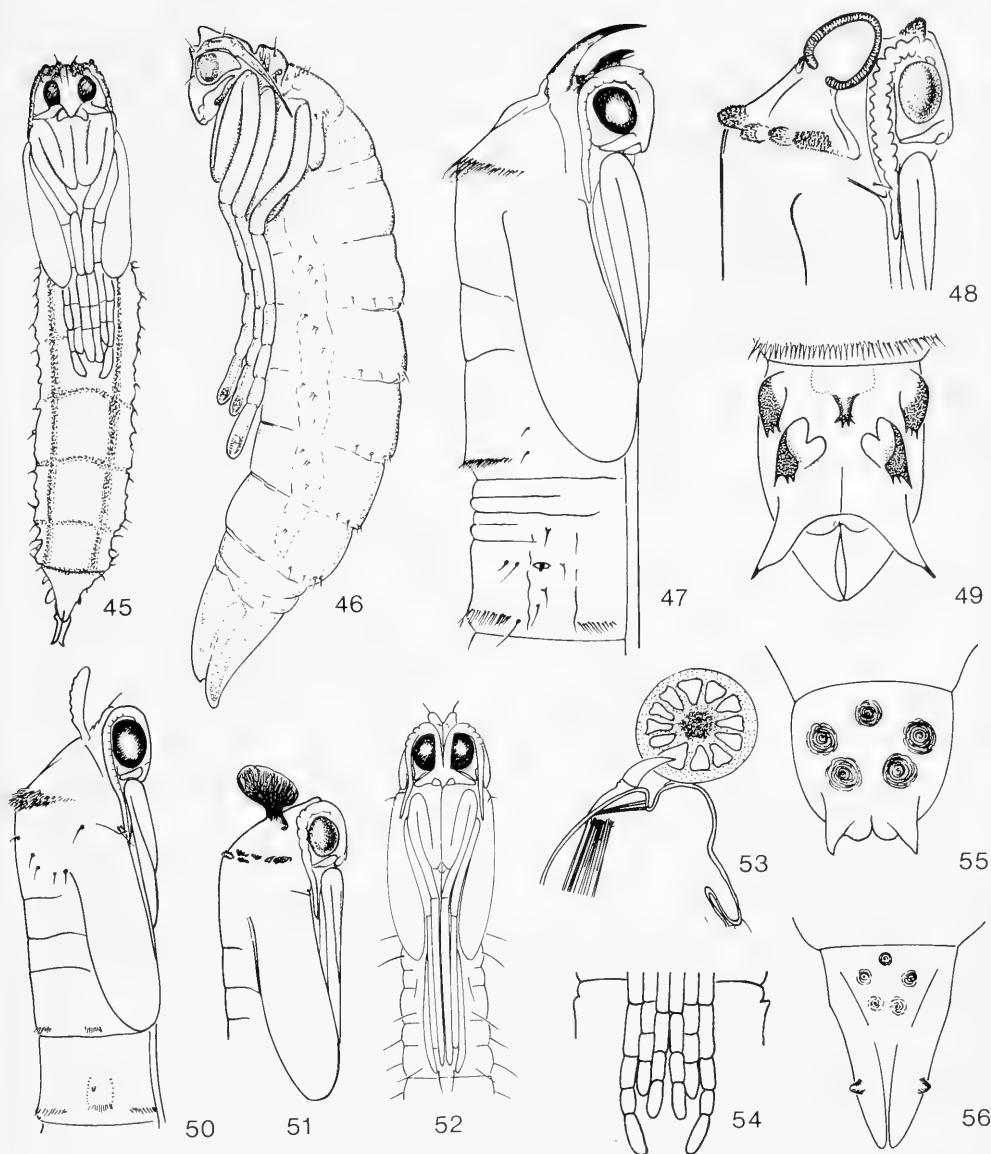
Crisp & Lloyd (1954) make the observation that, when the division of the dark markings (characters 44, 61, 62) is pronounced, the fringes are restricted to the tips of the spiracular lobes, whereas a slight division of the markings is associated with a complete hairfringe, representing the primitive condition.

56. Shape of mandible

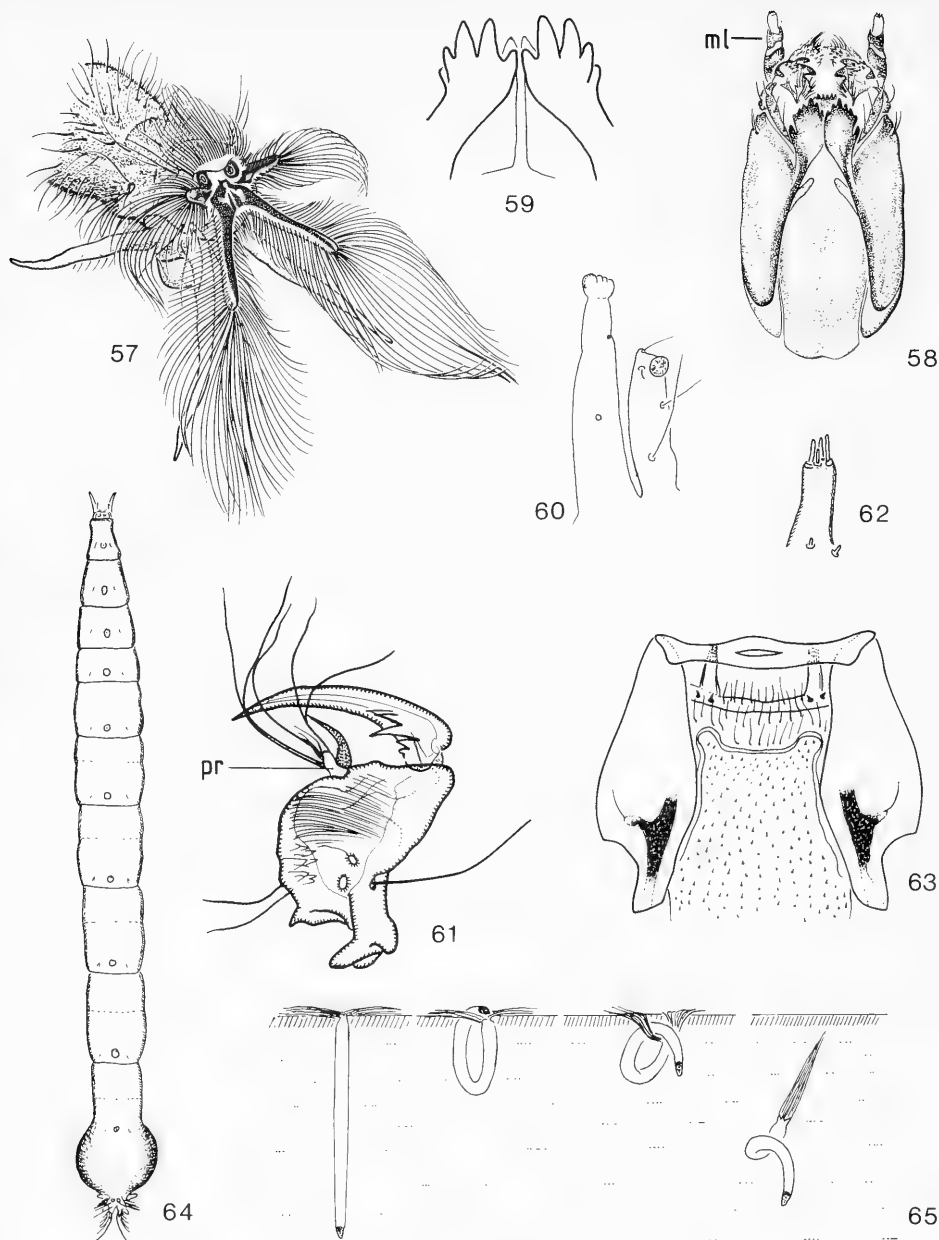
Ormosia and *Rhypholophus* are characterized by the identical shape of the mandibles (fig. 11). Similar shapes are not found among Tipuloidea but are present, as bifold mandibles, in several Psychodomorpha sensu Wood & Borkent 1989 (fig. 10). *Ormosia* and *Rhypholophus* do not represent the basal lineages of Eriopterinae. Therefore, the occurrence of similar mandibles in these two genera and in Psychodomorpha must be considered a convergent development.

57. Dark marking along inner margin of spiracles

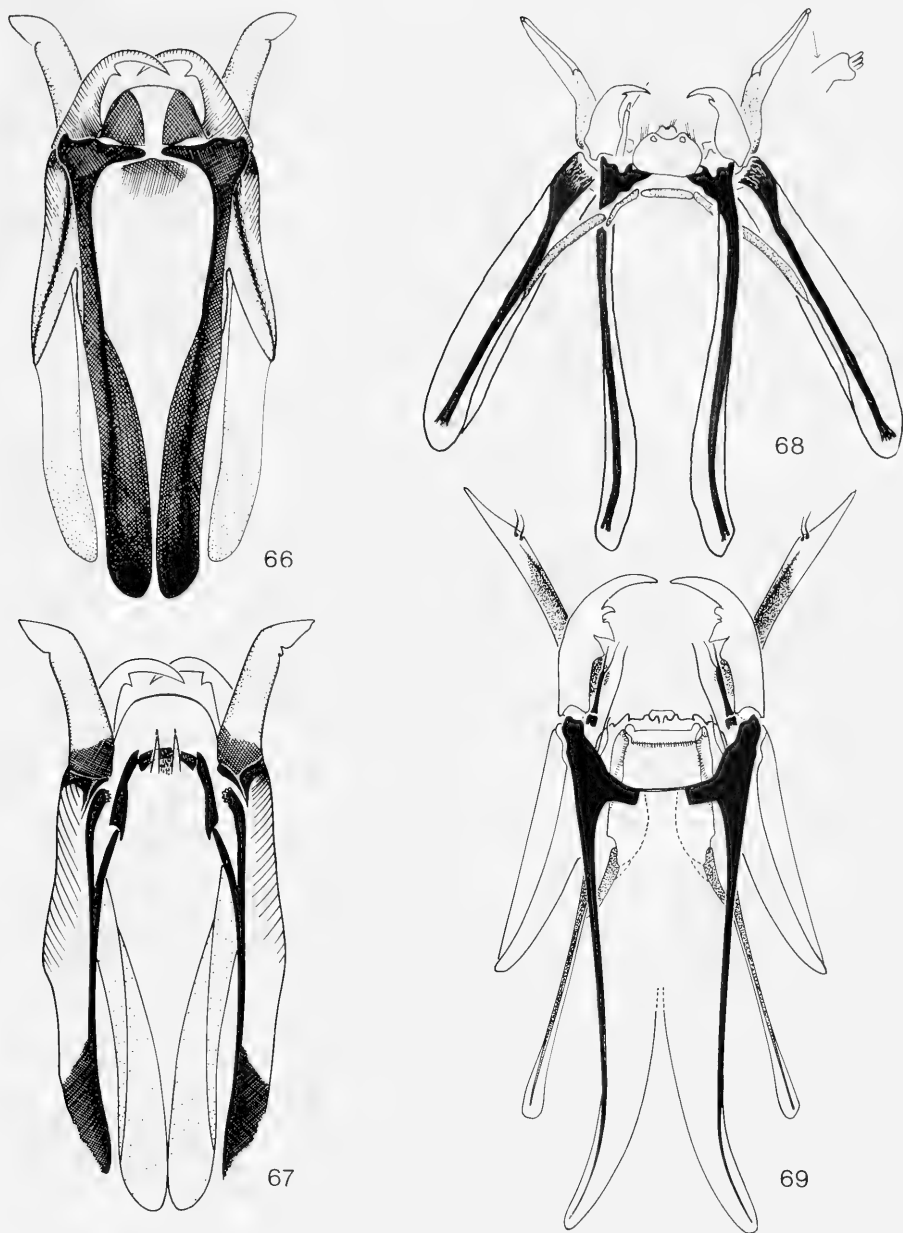
In *Arctoconopa*, *Erioconopa*, *Ilisia*, *Hoplolabis*, *Erioptera* and *Molophilus* the spiracular field is provided with a small dark marking along the



Figs. 45-56. Eriopterinae, pupal characters. - 45, *Eugnophomyia luctuosa*, female, ventral view; 46, *Chionea lutescens*, female, lateral view; 47, *Erioptera chlorophylla*, female, lateral view; 48, *Gonomyia alexanderi*, male, lateral view; 49, *Ormosia nigripila*, male cauda, dorsal view; 50, idem, male, lateral view; 51, *Gonomyia sulphurella*, female, lateral view; 52, *Teucholabis complexa*, male, ventral view; 53, longitudinal section through pupa of *Erioptera squalida*, showing insertion of respiratory horn into the gas space of a *Glyceria* root; 54, *Erioptera cladophoroides*, tarsal sheaths; 55, *Symplecta pilipes*, male cauda, dorsal view; 56, idem, female cauda, dorsal view (fig. 45: Rogers 1928; 46: Byers 1983; 47-52: Alexander 1920; 53: Houlihan 1969; 54: Bruch 1939; 55, 56: Wood 1952) (all figures redrawn).



Figs. 57-65. Hexatomiinae, larval characters. - 57, *Pseudolimnophila inornata*, terminal segment, oblique posterior view; 58, idem, head capsule (ml, outer maxillary lobe), ventral view; 59, *Paradelphomyia minuta* (supposition), hypostoma, ventral view; 60, idem, maxilla; 61, *Ulomorpha* spec., right mandible (pr, prostheca), dorsal view; 62, *Eloeophila maculata*, labial palp; 63, idem, hypopharyngeal skeleton, ventral view; 64, *Hexatoma* spec., larva, dorsal view; 65, *Limnophila* larva employing the head to stroke the long hairs of the spiracular disc free from the tension of the water surface (figs. 57, 58: Alexander & Byers 1981; 59, 60: Alexander 1920; 61: Anthon 1943a; 62, 63: Pokorný 1978; 64, 65: Lindner 1959) (all figures redrawn).



Figs. 66-69. Hexatomini, larval head capsules. – 66, *Eutonia* spec. (supposition), dorsal view; 67, idem, ventral view; 68, *Conosia irrorata*, ventral view, left dorsal bar interrupted to show hypopharyngeal skeleton, tip of right maxilla enlarged to show maxillary palp; 69, *Limnophila crepuscula*, dorsal view (Figs. 66, 67: Hennig 1950; 68, 69: Wood 1952) (all figures redrawn).

inner margin of the spiracles (fig. 31), not present in other Eriopterinae.

58. Ventral spiracular lobe without seta

The ventral spiracular lobes are usually provided with a distinct seta in most Tipuloidea (e.g. figs. 44, 136), but not in *Gonomyodes*, *Eriocnopa*, *Ilisia*, *Hoplolabis*, *Erioptera* and most species of *Molophilus*.

59. Ventral rods of head capsule not apically dentated

Hexatominae and Eriopterinae do not possess a complete hypostoma, but the ventral margins of the genae are still apically dentated in the lower representatives of these subfamilies (fig. 26). In the higher Eriopterinae the ventral rods of the head capsule (which are homologous with the ventral margins of the genae) are usually not dentated (fig. 12) except for some species of *Rhabdomastix* (Hynes 1969c: fig. 8) and for *Erioptera* and *Molophilus* (fig. 13), which possess a similar hypostoma, not found in other Eriopterinae. Therefore, return to the plesiomorphic condition is interpreted as a synapomorphy for the two last-mentioned genera.

60. Penultimate segment of larvae inflated

Larvae of several Eriopterinae are recorded to be able to inflate the penultimate segment (fig. 36). Inflation is usually less conspicuous, although Wood (1952) records distinct inflation as in Hexatominae for *Rhabdomastix afra* (see also character 26).

61. Dorsal spiracular marking divided into two

62. Lateral spiracular markings divided into two

Apart from divided ventral markings (character 44), the markings on the dorsal and/or lateral spiracular lobes can be divided into two as well.

6. HEXATOMINAE

Introduction

The name Hexatominae is used here in a more restricted sense than in the current systematic literature (chapter 4, Introduction). The genera *Paradelphomyia* and *Pseudolimnophila* are treated here as lower Hexatominae and all other genera of which larvae and/or pupae are known as higher Hexatominae. *Paradelphomyia* is usually assigned to the small tribe Paradelphomyiini, whereas *Pseudolimnophila* is included in the large tribe Limnophilini.

In Hexatominae the spiracular field usually possesses four elongate flattened lobes with the ven-

tral ones the longest, sometimes with a vestigial fifth lobe. The spiracular field is usually provided with long hairs, especially towards the tips of the elongate ventral lobes (figs. 57, 70, 71). By means of these long hair fringes the larva can hold air when submerged, or be freely suspended. The effectiveness of holding the spiracular disc at the surface of the water can be so great, that the larva may have to curl over the spiracular disc in order to break the suspension (fig. 65).

Four elongate, cylindrical instead of flattened lobes with the ventral ones the largest are also present in *Cryptolabis* (figs. 28, 29) and more or less in *Baeoura* (fig. 27). According to Hynes (1963), presence of elongate spiracular lobes in *Cryptolabis* and, for example, *Eloeophila* must be considered an adaptation to the habitat of the larvae, which live in sand and gravel of swiftly flowing waters. Elongate flattened spiracular lobes with the ventral lobes the longest is nevertheless not listed as a synapomorphy for the Hexatominae because it might as well be considered a synapomorphy for Eriopterinae plus Hexatominae. No other characters are available to base upon the monophyly of the Hexatominae.

The very similar hypostomal plates of *Paradelphomyia* (fig. 59) and *Pseudolimnophila* (fig. 58) are not found among other Tipuloidea, but the similarity might be symplesiomorphic (see character G).

Most Hexatominae are predators on insect larvae, oligochaetes, copepods and the like. Their method of feeding is discussed by Crisp & Lloyd (1954) and a detailed description of a 10 mm *Limnophila* larva engulfing a 15 mm oligochaete is given by Lindner (1959). *Pseudolimnophila* is a gross feeder of plant remains, diatoms and small algae. Species of *Paradelphomyia* and *Neolimnomyia* are believed to be feeders on animal protein, but are not always predacious or carnivorous (Crisp & Lloyd 1954, Hinton 1954, Brindle 1967).

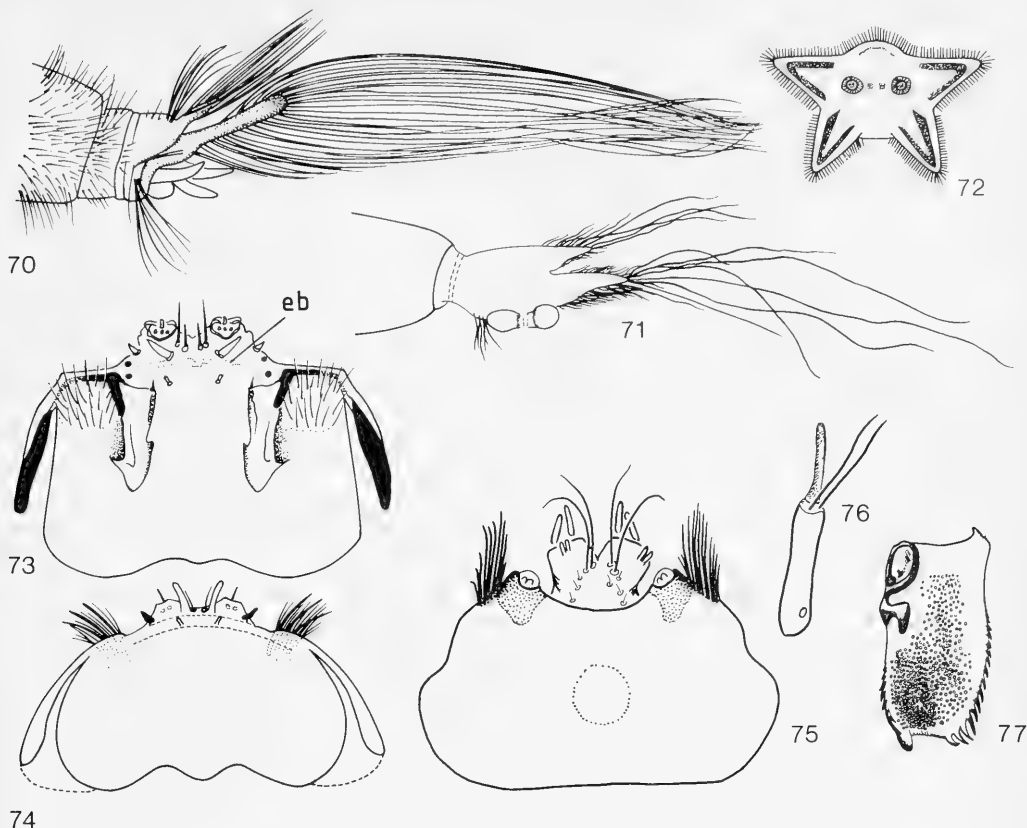
Characters

63. Setae in front of anal papillae

In Hexatominae the last abdominal segment of the larvae ventrally bears distinct setae in front of the anal papillae, either arranged in groups (Wolff 1922), or as a distinct row (figs. 70, 71, 79-81). Information about these setae, which are absent in other Tipuloidea except for some species of *Elephantomyia* (see chapter 9), is not available for *Paradelphomyia*, *Polymera* and *Neolimnomyia*.

64. Tufts of hair on labrum

The labrum of larvae of Hexatominae, *Paradelphomyia* excepted, is provided with distinct tufts of



Figs. 70-77. Hexatomiinae, larval characters. – 70, *Eutonia* spec. (supposition), terminal segment, lateral view; 71, *Conosia irrorata*, terminal segment, lateral view; 72, *Neolimnomyia nemoralis*, spiracular disc; 73, *Eloephila submarmorata*, labrum, dorsal view, showing large sclerotized plates on ventral surface caudal to epipharyngeal bar (eb); 74, *E. dubiosa*, labrum, dorsal view; 75, *Conosia irrorata*, labrum, dorsal view; 76, *Pseudolimnophila lucorum*, antenna; 77, *Hexatoma cinerea*, left hypopharyngeal plate, ventral view (fig. 70: Hennig 1950; 71: Wood 1952; 72: Brindle & Bryce 1960; 73: Pokorný 1978; 74, 75: Wood 1952; 76: Rozkosný & Pokorný 1980; 77: Alexander 1920) (all figures redrawn).

hair on the antero-lateral sides (figs. 73-75). These tufts are not found in other Tipuloidea. It is not known whether they are present in *Neolimnomyia* or *Eutonia*.

65. Reduction of the inner maxillary lobe

In *Paradelphomyia* two distinctly separated maxillary lobes are present (fig. 60). In the other Hexatomiinae there is a tendency to reduction of the inner lobe through fusion with the outer lobe (details in Crisp & Lloyd 1954, Pokorný 1978; reduction of the inner lobe occurred also in several Pediciini, *Cryptolabis* and *Rhabdomastix*).

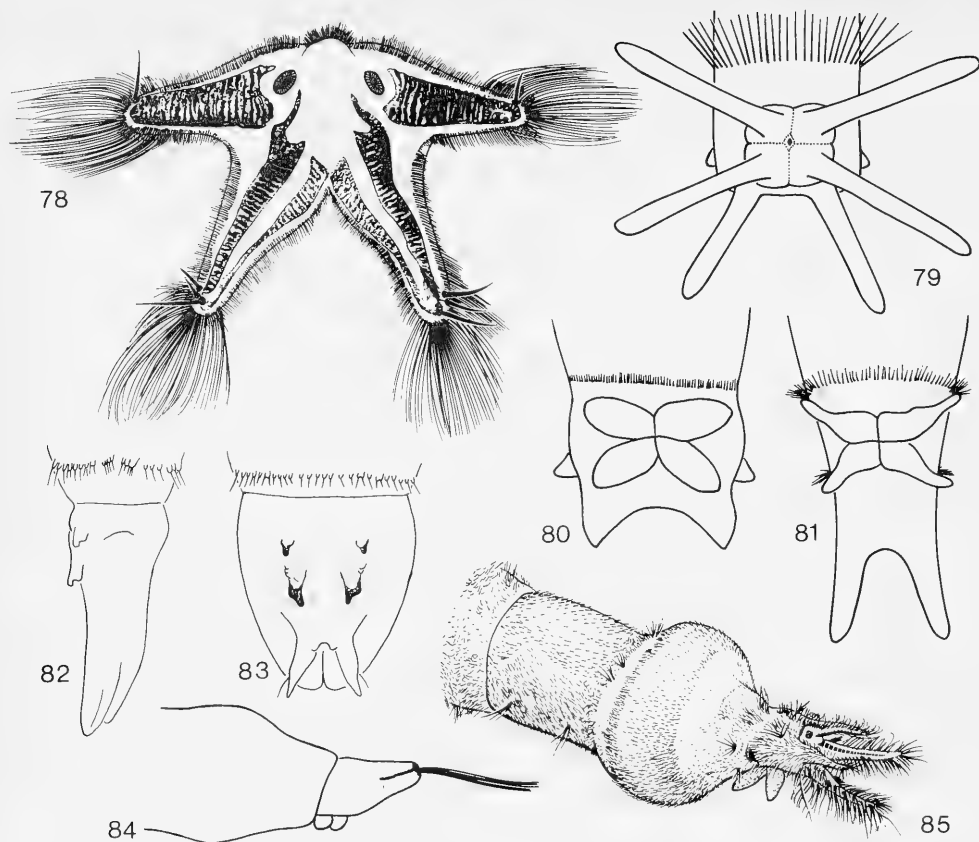
66. Mandible sickle shaped

The mandibles of higher Hexatomiinae are sickle shaped with a long terminal point and shorter teeth about half-way down the blade (figs 61, 66-

69). A similar mandible is found in a number of Pediciini, probably as an adaptation to predation. The more generalized type of mandible, as in most other Tipuloidea including *Paradelphomyia* and *Pseudolimnophila*, usually has a strong row of teeth along the ventral edge and a weaker row along the dorsal edge (figs. 115, 125, 128, 138).

67. Head capsule further reduced

The reduced head capsule of higher Hexatomiinae does not show a dentated hypostoma divided along the midline as in *Paradelphomyia* and *Pseudolimnophila*, but the ventral rods possess medial side branches which articulate with the very typical hypopharyngeal skeleton. This skeleton consists of two large lateral plates and a transverse bar. This bar is perforated by an orifice and provided with very small teeth (figs. 63, 67-69). Furthermore,



Figs. 78-85. Hexatomiinae, larval and pupal characters. – 78, *Eutonia barbipes*, spiracular disc; 79, *Pseudolimnophila lucorum*, terminal segment, ventral view; 80, *Euphyllidorea lineola*, terminal segment, ventral view; 81, *Pilaria discicollis*, terminal segment, ventral view; 82, *Limnophila fuscovaria*, female cauda, lateral view; 83, idem, male cauda; 84, *Neolimnomyia batava*, terminal segments, lateral view; 85, *Limnophila* spec., terminal segments, oblique posterior view (fig. 78: Wolff 1922; 79-81: Savchenko 1986; 82, 83: Alexander 1920; 84: Brindle & Bryce 1960; 85: Alexander & Byers 1981) (all figures redrawn).

well developed labial papillae are present (figs. 62, 63, 67). The hypopharyngeal skeleton is absent in *Pilaria*, *Ulomorpha* and several species of *Hexatoma* whereas other species of *Hexatoma* possess large lateral plates (fig. 77) but lack the transverse bar.

68. Statocysts

As in higher Eriopterinae, statocysts are present in larvae of higher Hexatomiinae. According to Wolff (1922) and Crisp & Lloyd (1954) they are not present in *Paradelphomyia* and *Pseudolimnophila*, while no information is available for *Ulomorpha*, *Polymera*, *Neolimnomyia* and *Conosia* (see also character 54).

69. Caudal end of dorsal plates spatulate

70. Mandible bifid

Pilaria and *Ulomorpha* are without doubt sister-

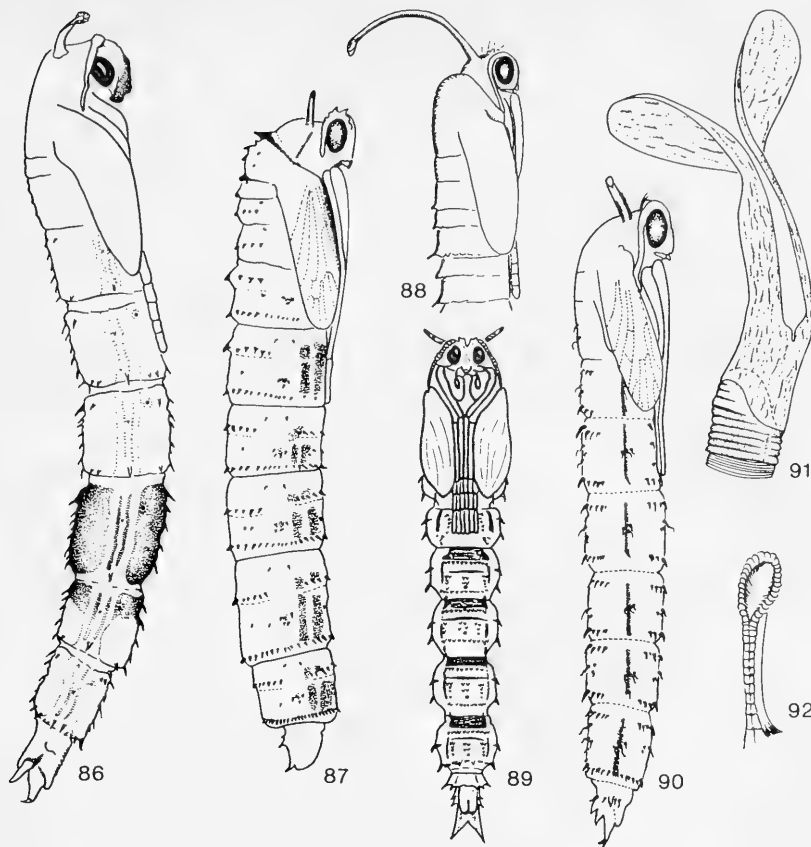
groups on the basis of the above two characters. The very characteristic bifid mandibles (fig. 61) and the absence of any rigidity in the ventral region of the mouth are associated with the method of feeding on worms as described by Crisp & Lloyd (1954).

71. Maxilla narrowed towards tip

The apex of the outer lobe of the maxillae is blunt in *Paradelphomyia* (fig. 60), *Pseudolimnophila* (fig. 58), *Pilaria* and perhaps also *Ulomorpha*. In the other Hexatomiinae the maxillae are narrowed towards the tips with a very characteristic outward orientation of the apical part (figs. 66-69).

72. Dorsal bridge divided

The dorsal plates of the head capsule are still fused in *Pilaria* and *Ulomorpha* (Alexander 1920)



Figs. 86-92. Hexatominæ, pupal characters. – 86, *Conosia irrorata*, male, lateral view; 87, *Limnophila crepuscula*, male, lateral view; 88, *Ulomorpha pilosella*, female, lateral view; 89, *Eloeophila maculata*, female, ventral view; 90, *E. dubiosa*, male, lateral view; 91, *Pseudolimmophila lucorum*, apical flaps of respiratory horn; 92, *Conosia irrorata*, respiratory horn (figs. 86, 87, 90, 92: Wood 1952; 88: Alexander 1920; 89: Pokorný 1978; 91: Hinton 1954) (all figures redrawn).

but are separated and variously modified in the other higher Hexatominæ (figs. 66, 68, 69). The description and figures by Rogers (1933) for *Polymera* can not be interpreted adequately but the dorsal plate is apparently divided (with large lateral plates as in *Hexatoma*?, see Rogers 1933: fig. 2).

In the *Polymera-Eutonia* lineage the anal papillae are short (figs. 64, 70, 71, 80, 84, 85) compared to the very elongate papillae of *Paradelphomyia*, *Pseudolimmophila*, *Pilaria* and *Ulomorpha* (figs. 57, 79). This character might be considered a weak synapomorphy as well. Some species of *Pilaria*, however, can have the papillae less elongate (fig. 81), whereas they are elongate in *Hexatoma spinosa* (Byers 1978: fig. 19.17).

73. Apex of respiratory horn not flap-like

In *Pseudolimmophila*, *Pilaria*, *Ulomorpha* and

Polymera the respiratory horns are provided with apical flaps (figs. 88, 91). This character is interpreted as belonging to the groundplan condition in Hexatominæ except *Paradelphomyia*, with secondary loss in part of the higher Hexatominæ (see also chapter 4, Respiratory horns).

74. Respiratory horn shortened

In the *Phylidorea-Eutonia* lineage (figs. 86, 87, 89, 90) the respiratory horns are much shorter than in *Paradelphomyia* and the genera with flap-like respiratory horns. The only exception are species of *Neolimnomyia* (*Neolimnomyia*) which also possess elongate respiratory horns. In *Phylidorea*, *Euphylidorea*, *Eloeophila* and several species of *Limnophila* the organ is laterally compressed. In some *Hexatoma* species they are acute (see also chapter 4: Respiratory horns.).

75. Pupal abdominal segment 7 with spined tubercles

In a number of higher Hexatominæ the seventh abdominal segment of the pupæ is provided with many spined tubercles surrounding the caudal end of the segment (figs. 82, 83). It is not known whether this character is present in *Polymera*. It is apparently absent in *Neolimnomyia*.

76. Last abdominal segment constricted

In *Limnophila*, *Neolimnomyia*, *Conosia* and *Eutonia* the last abdominal segment is constricted. This character is listed as a synapomorphy for the Eriopterinae but apparently does not belong to the groundplan condition of Hexatominæ.

77. Respiratory horn club-shaped

78. Mandible single toothed in the middle

Conosia and *Eutonia* are considered sistergroups on the basis of their club-shaped respiratory horns (figs. 86, 92) and single toothed mandibles (figs. 66-68). The latter character occurs also in some species of *Hexatoma* (Alexander 1920).

79. Larval creeping welts

Dorsal and ventral creeping welts on segments 5-10 are found in larvae of *Eloeophila*, *Limnophila* (*Lasiomastix*) *macrocera*, *Conosia*, *Eutonia* and apparently also *Neolimnomyia* (*Brachylimnophila*) (see Beling 1886).

80. Markings on ventral spiracular lobes divided into two

This character is present in *Paradelphomyia* and a number of higher Hexatominæ including *Neolimnomyia* (*Brachylimnophila*) (figs. 57, 72, 78). It does not occur in all species of *Limnophila* and is unknown for *Neolimnomyia* (*Neolimnomyia*) where the spiracular disc seems to be permanently closed (fig. 84; Brindle & Bryce 1960).

81. Pupal abdominal segments with lateral carina

Distinct lateral carinae provided with spines (fig. 89) are present on the abdominal segments of the pupæ of *Pilaria*, *Phylidorea*, *Euphyllidorea*, *Eloeophila*, *Neolimnomyia* and several species of *Limnophila*.

82. Penultimate segment of larvae inflated

Among Hexatominæ inflation of the penultimate segment seems to be weak or absent in a number of genera. Distinct inflation is known to occur in *Paradelphomyia*, *Pilaria*, *Phylidorea*, *Euphyllidorea*, *Eloeophila* (fig. 85), *Hexatoma* (fig. 64) and *Limnophila*.

7. PEDICIINAE

Introduction

Pediciinae is a small subfamily, divided in two tribes, Ulini and Pediciini. The larvae of *Ula* (Ulini) feed on fungi. The larvae of the other genera discussed here belong to the Pediciini and are predators on oligochaetes, mites, insect larvae and the like (details in Crisp & Lloyd 1954 and Lindner 1959). Because of the very massive head capsule, Pediciini are not able to swallow large prey as a whole but have to tear them to pieces (Lindner 1959). Pupæ of Pediciinae are enclosed in a substantial silken tube covered with detritus, as in Limoniinae (character 9).

The adopted phylogeny (fig. 7) shows two groups of *Tricyphona*. The palaearctic species *T. immaculata*, *T. schummeli* and *T. unicolor* are included in *Tricyphona* 1; *T. inconstans* from the Nearctic represents *Tricyphona* 2. *Rhaphidolabina*, generally placed as a subgenus of *Dicranota* (Savchenko et al. 1992), is placed as sistergroup of *Tricyphona* 2.

Characters

83. Cardo reduced

In Pediciini the cardo is reduced to a small plate (fig. 100). The reduced inner lobe of the maxilla is closely aligned to the outer lobe. According to Crisp & Lloyd (1954) reduction of the inner lobe is less in *Pedicia rivos*a, intermediate in *Tricyphona* spec., and most obvious in *Dicranota bimaculata*. The available information on the other species and genera does show that reduction of the inner lobe is rather variable and apparently not linked to the adopted phylogeny.

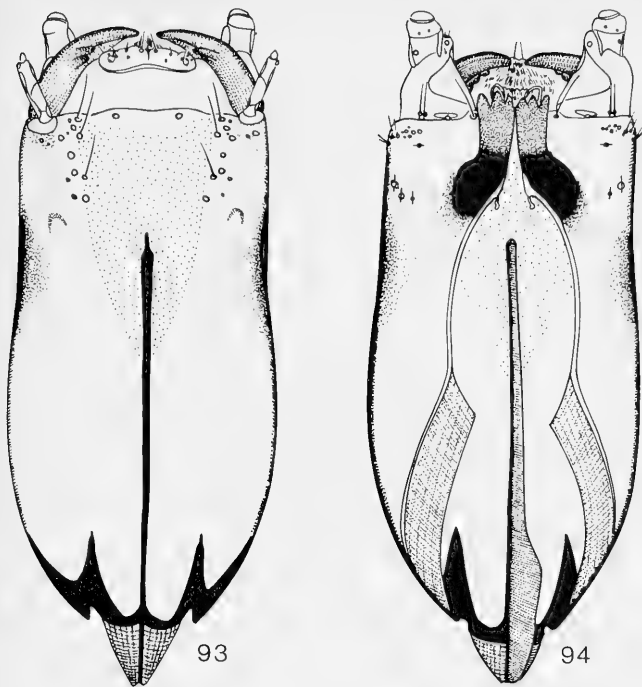
84. Larvae with ventral creeping welts on sternites 6-10 or 7-10

Ventral creeping welts on the anterior part of sternites 5-10 is interpreted as the plesiomorphic condition in Tipuloidea (character 29). In Pediciini welts are present on sternites 7-10 (figs. 107, 108), or as pseudopods in *Rhaphidolabis*, *Paradicranota* and *Dicranota* on sternites 6-10 (fig. 104). On the basis of characters 88 to 94 it is assumed that the number of welts decreased from six to four in Pediciini with an increase to five in the *Rhaphidolabis-Dicranota* lineage. Of interest is the presence of welts on segments 5-10 in the apparently primitive pediciine genus *Sigmatomera* (see chapter 9).

85. Hypostomal plates with three or four teeth

86. Two parts of hypostoma with a push-button connection

The hypostoma of Pediciini is very characteristic



Figs. 93-94. Head capsule of *Tricyphona immaculata*. – 93, dorsal view; 94, ventral view (Lindner 1959) (figures redrawn).

(fig. 97). It is divided along the midline, each half with three or four teeth and the two parts are held together with a push-button connection. Usually one or two buttons are present, in *Tricyphona* 2 there are three. A similar connection is present in *Pedicia*, but without a clear separation in push-buttons.

- 87. Spiracular field with prominent ventral lobes.
- 88. Ventral spiracular lobes very elongate

In *Pediciini* only the ventral spiracular lobes are prominent (figs. 105-108), and very elongate except for *Tricyphona* 1 (figs. 105, 107). The ventral lobes terminate with a group of setae at the end.

- 89. Mandible sickle shaped

As in higher Hexatominae (character 66), the mandibles of *Pediciini* are sickle shaped (fig. 102), *Tricyphona* 1 excepted (fig. 101). They are provided with four large ventral teeth and the lower ventral tooth is always the largest and more or less rectangular.

- 90. Spiracular field small and spiracles close together

The spiracular field in *Tricyphona* 1 is large with the spiracles far apart (fig. 105), as in *Ula* and the other genera of the *Dactylolabis*-*Tipulidae* lineage. In the remaining *Pediciini* the spiracular field is small and the spiracles are close together (fig. 106).

- 91. Creeping welts concave in the middle

The creeping welts of *Tricyphona* 1 are as found in the other *Tipuloidea*. In the remaining *Pediciini* they are laterally elevated into humps or pseudopods (fig. 104; character 95).

- 92. Pupal pleura with circular areas of spicules

The abdominal pleura of the pupae of *Tricyphona* 2 and *Rhaphidolabina* are provided with large, circular areas of short rows of microscopic spicules. It is not known whether this character is present in *Tricyphona* 1.

- 93. Hypostomal plates with four teeth

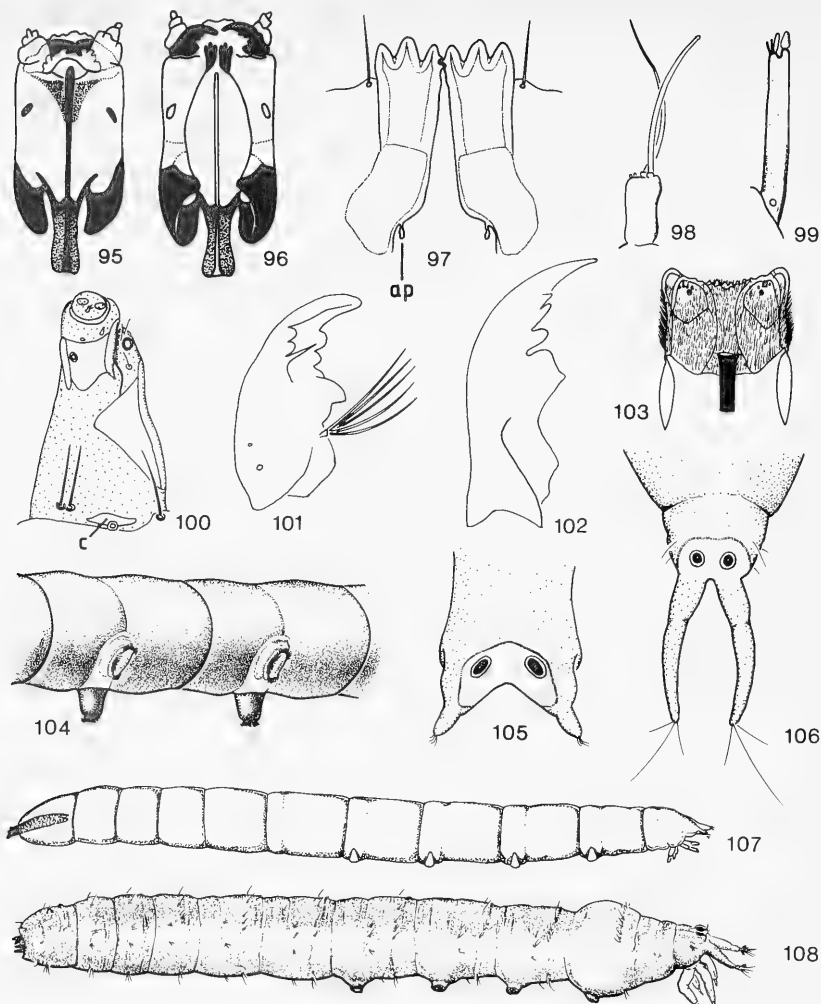
Each hypostomal plate in *Tricyphona* 2 and *Rhaphidolabina* is provided with four teeth, whereas the other *Pediciini* possess three teeth.

- 94. Spiracles on elevations

Pedicia, *Rhaphidolabis*, *Paradicranota* and *Dicranota* larvae have the spiracles situated on small elevations (fig. 108), a character not found among other *Pediciinae* or *Tipuloidea*. The small elevations are interpreted by Crisp & Lloyd (1954) as representing the lateral spiracular lobes.

- 95. Pseudopods

Pseudopods, apically set with rings of recurved hooklets (fig. 104) are found in the larvae of *Rhaphidolabis*, *Paradicranota* and *Dicranota*. They are



Figs. 95-108. Pediciini, larval characters. – 95, *Tricyphona immaculata*, head capsule of first instar, dorsal view; 96, idem, ventral view; 97, *T. immaculata*, hypostoma (ap. apophyse), ventral view; 98, *Dicranota (Rhabidolabina) flaveola*, antenna; 99, *Dicranota (Dicranota) bimaculata*, antenna; 100, *T. immaculata*, right maxilla (c, cardo), ventral view; 101, idem, left mandible, dorsal view; 102, *Pedicia rivos*, left mandible, dorsal view; 103, *T. immaculata*, prementum, ventral view; 104, *Dicranota (Paradicranota) subtilis*, creeping welts (pseudopods) of segments 8 and 9; 105, *T. immaculata*, terminal segment, dorsal view; 106, *Dicranota spec.*, terminal segment, dorsal view; 107, *T. immaculata*, larva, lateral view; 108, *Pedicia spec.*, larva, lateral view (fig. 95, 96: Okely 1979; 97, 100, 101, 103-105, 107: Lindner 1959; 98: Alexander 1920; 99: Reusch 1988; 102: Wardle & Taylor 1926; 106: Savchenko 1986; 108: Alexander & Byers 1981) (all figures redrawn).

present on the anterior part of sternites 6-10. The only other genus of Tipuloidea with pseudopods is *Aphrophila* (see chapter 9).

96. Pupae with ventral creeping welts

Pupae of *Rhabidolabis* are not known. Those of the other taxa possess dorsal creeping welts, situated more lateral in *Paradicranota* and *Dicranota*. Ventral creeping welts are present in *Tricyphona* and *Pedicia*, whereas in *Paradicranota* and *Dicranota* the sternites are provided with fleshy projec-

tions, corresponding with the larval pseudopods and used to assist the movements of the pupa through the mud (Miall 1893).

97. Apical papillae of antenna reduced

Pediciinae usually have the larval antenna provided with two distinct apical papillae (figs. 98, 114; character 7). In *Rhabidolabis* and *Dicranota* the papillae are short (fig. 99; Alexander 1920, Reusch 1988) and in *Tricyphona immaculata* only one short papilla is present (information for the

other species assigned to *Trichypona* 1 is not available).

98. Basal segment of antenna short

The basal antennal segment of Tipuloidea larvae is usually well developed, but short in *Ula* (fig. 114) and some species of *Dactylolabis* (see character 7). In Pediciini the basal segment is elongate (fig. 99) except for *Tricyphona* 2 and *Rhaphidolabis* (fig. 98) with a length intermediate between *Ula* and the other Pediciini.

8. LIMONIINAE

Introduction

Palearctic genera of Limoniinae are divided into two tribes, Antochini and Limoniini (Diencke 1987, Savchenko et al. 1992). This division is also apparent on the basis of immature characters. In figure 8 the genera *Atypophthalmus* to *Discobola* belong to the Limoniini, the others to the Antochini.

The phylogenetic arrangements of the genera dealt with is based on few characters and distinct sistergroup relations within the Limoniini could not be established. This is at least of some interest because genera of Limoniini are usually considered subgenera of *Limonia* by most North American and British workers. It appears that, as far as character polarities could be established within the Limoniini, all character-states are present in representatives of the large genus *Dicranomyia*.

Limoniinae larvae are herbivorous, feeding on decayed plant material, diatoms, organic mud and the like. Larvae of several species live in fungi (Lindner 1958). Experiments to find out their preferences for leaf-litter of different deciduous trees are described by Lindner (1959).

Characters

99. Larvae in tube or case

Unlike other Tipuloidea, larvae of Limoniinae live inside silken or gelatinous tubes, usually covered with detritus, silt or diatoms, some species of *Dicranomyia* excepted (Wood 1952: *D. peringueyi*, Brindle 1967: *D. didyma*). *Thaumastoptera* larvae live in a dark grey or blackish hardened elliptical flattened case. Information is not available for *Atypophthalmus*.

100. Pupal creeping welts elliptical

In the Limoniinae the pupal creeping welts are distinctly elliptical, a character not found in other Tipuloidea. The central part of the welts is frequently naked or bears a reduced number of spicules (figs. 157-159).

101. Spiracles oblong or elliptical

102. Spiracles placed obliquely

Antocha larva are apneustic, without spiracles. The spiracles of the other Limoniinae are oblong or elliptical and placed obliquely (figs. 141, 142, 150). These two characters must be considered weak synapomorphies because they are found, albeit less pronounced, in several other Tipuloidea (figs. 78, 105, 136).

103. Larval segments 2 to 10 with creeping welts

In addition to the creeping welts present on segments 5-10, the genera included in the Limoniini and *Elliptera* possess creeping welts, but with a lower relief, on the anterior margin of segments 2, 3 and 4 and the posterior margin of segment 10 (figs. 143, 144). It is not known whether this character is present in *Atypophthalmus*.

104. Spiracular lobes reduced

Limoniini have the spiracular lobes reduced and very frequently they are indicated only by the dark patches of chitization or by the general outline of the spiracular field (figs. 141-144).

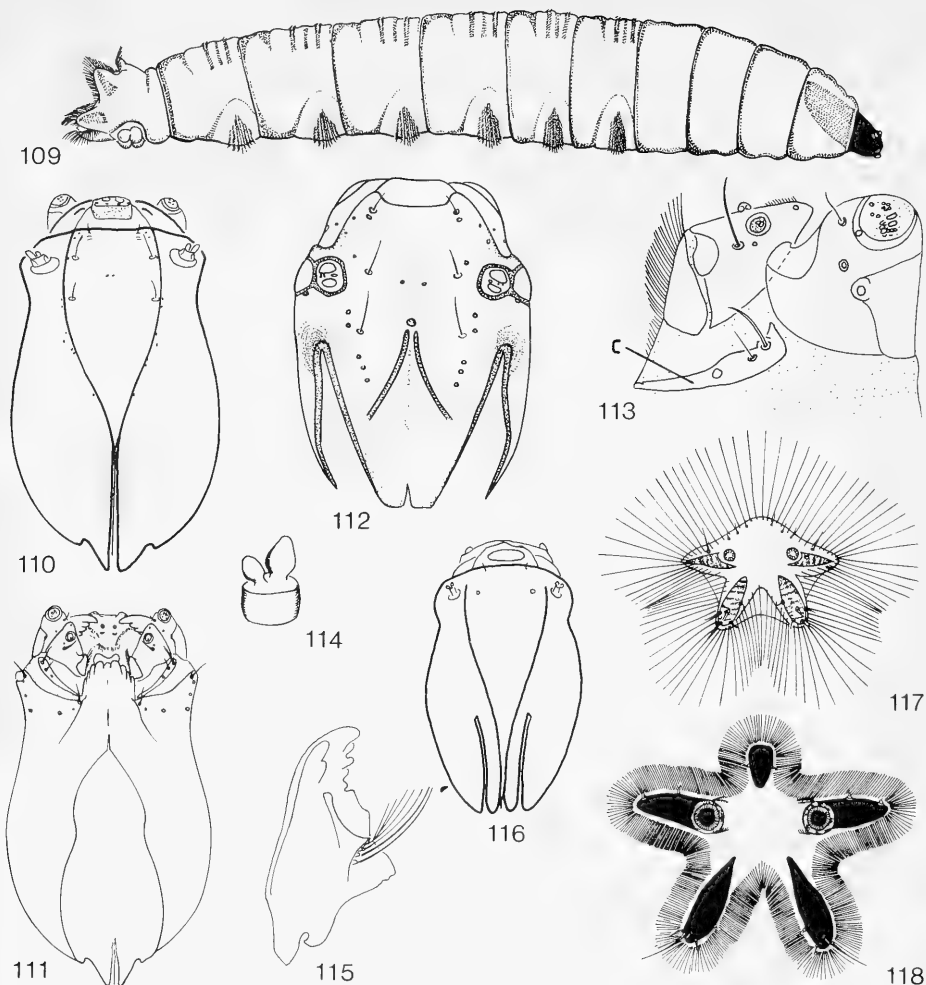
105. Caudal end of head capsule tridentate

Only in Limoniini the caudal end of the head capsule is tridentate (figs. 139, 140). The space between the lateral and central points is interpreted by Lindner (1959) as remnants of the frontal sutures. This character remained unknown for *Atypophthalmus* and is not present in all species of *Limonia*.

9. REMAINING GENERA

Discussed below are a number of genera which could not be incorporated among the genera mentioned in figs. 4-8 because of the limited, or in some cases controversial, information available. The current systematic position of the taxa is given in parentheses.

Aphrophila (Eriopterinae). – Winterbourn & Gregson (1989) figure the larva of *Aphrophila neozelandica*, which is very aberrant compared to the known larvae of Eriopterinae. The last abdominal segment appears constricted (character 36) and the head capsule is dissected (character 49). Spiracular lobes are absent (character 41) and the larva seems to be apneustic. Unlike other Eriopterinae, dorsal creeping welts ('scars') are present on tergites 6-10. Sternites 5-10 also possess creeping welts (character 48), but shaped as pseudopods very similar to the pediciine taxa *Rhaphidolabis*, *Paradicranota* and *Dicranota* (character 95).



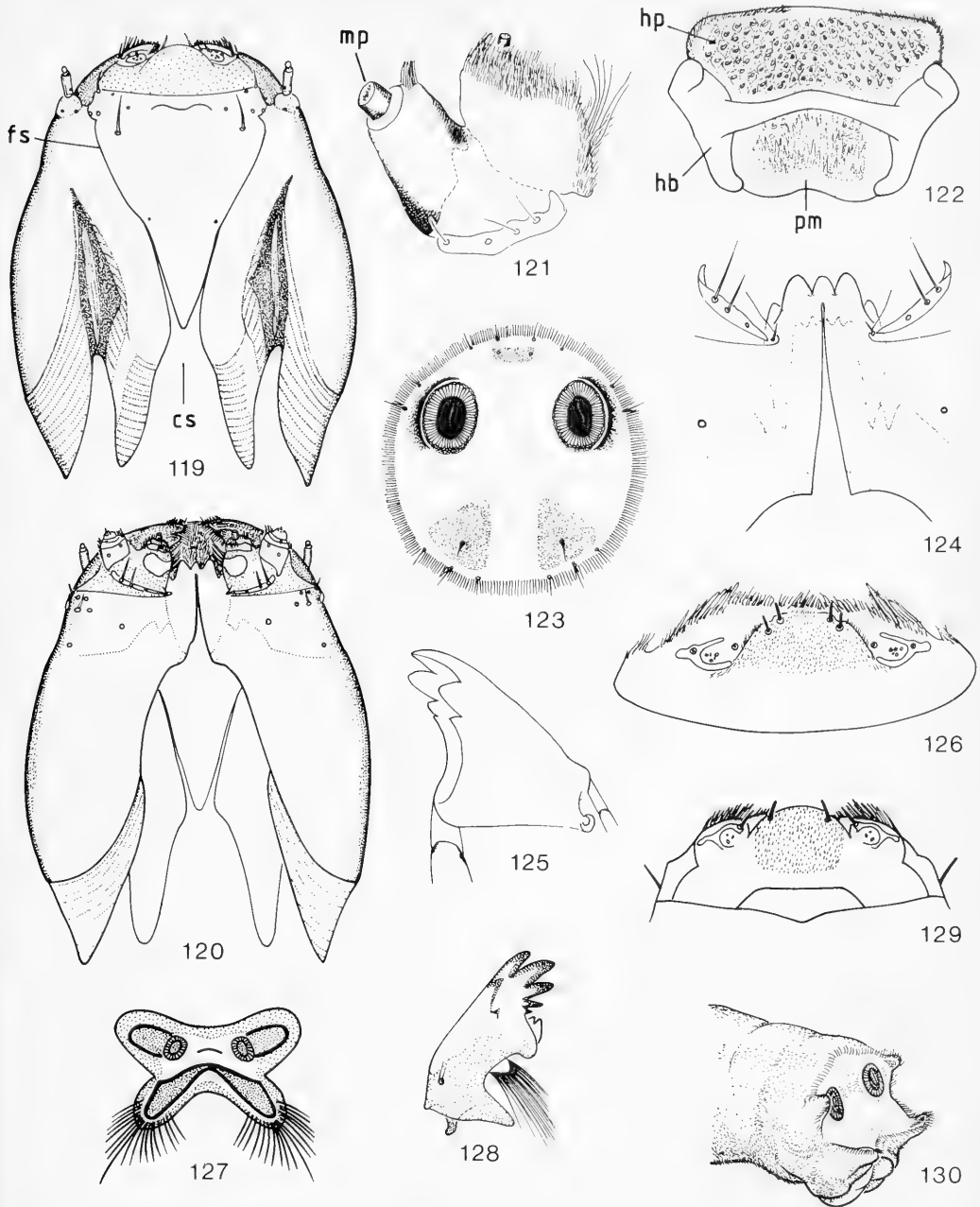
Figs. 109-118. *Ula*, larval characters. – 109, *U. mollissima*, larva, lateral view; 110, idem, head capsule, dorsal view; 111, idem, ventral view; 112, *U. sylvatica*, head capsule of first instar larva, dorsal view; 113, *U. mollissima*, left maxilla (c, cardo), ventral view; 114, *U. elegans*, antenna; 115, *U. mollissima*, left mandible, dorsal view; 116, *U. sylvatica*, head capsule, dorsal view; 117, idem, spiracular disc of first instar larva; 118, *U. mollissima*, spiracular disc (figs. 109-113, 115, 117, 118: Lindner 1959; 114: Alexander 1920; 116: Bryce 1957b) (all figures redrawn).

Gonempeda (Eriopterinae: Eriopterini). – The only original figures of the pupa of *Gonempeda flava* are those by Brindle (1967, as *Cheilotrichia*) and only a few characters can be interpreted. The respiratory horns are not earshaped and the mesonotal crest seems to be lacking (characters 38, 46 and 50 not present).

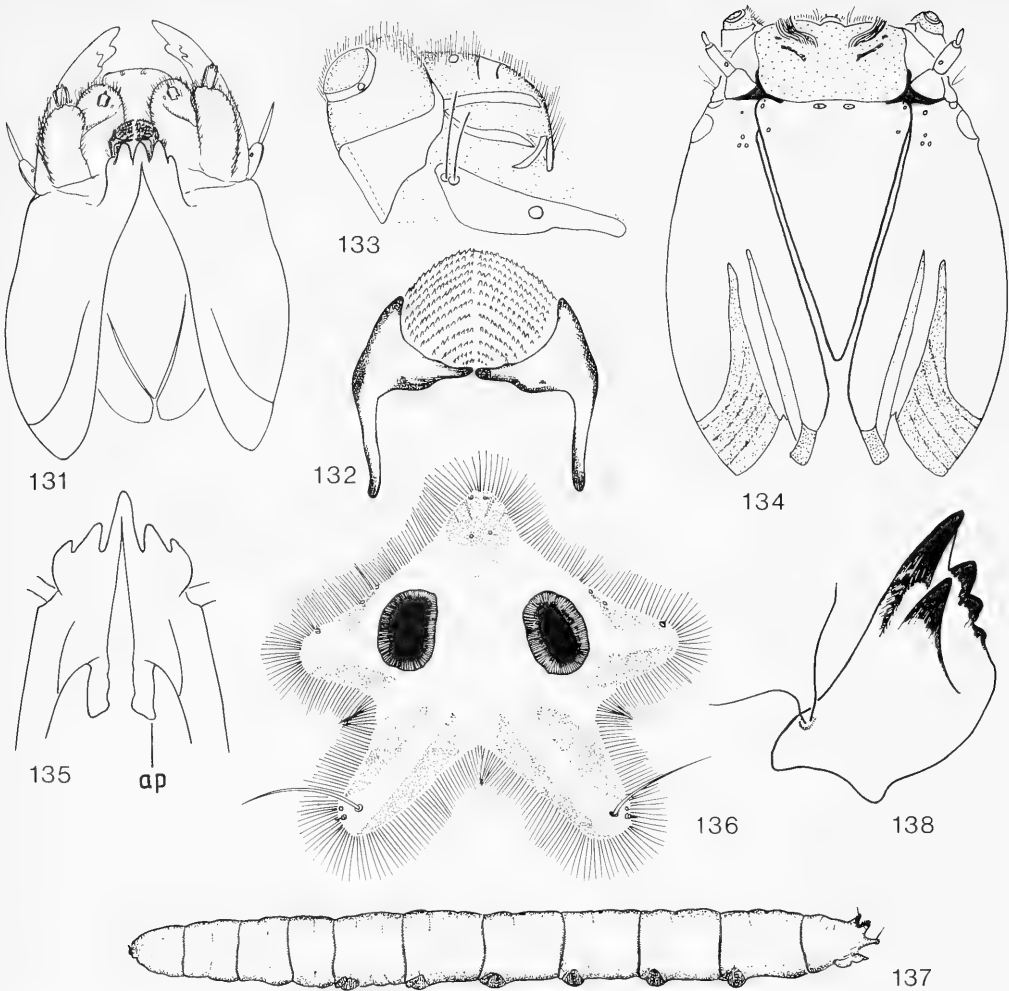
Hesperoconopa (Eriopterinae: Molophilini). – The larva and pupa of *Hesperoconopa dolichophallus* are described and figured by Hynes (1968). The unique terminal segment of the larva is setulose, elongate cone shaped and bifurcate at the extreme tip, lacking spiracles. Information is avail-

able for the following characters: Present are 36, 38, 41 (but abdominal end quite different from *Cladura* and *Chionea*), 49 and 59 (ventral bars not apically toothed). Not present are 42 (palpsheaths appear upcurved), 48, 50 and 53.

Neolimnophila (Eriopterinae: Cladurini). – Beling (1886) presents a description of the larva and pupa of *Neolimnophila carteri* (as *Limnophila hyalipennis*). The pupal respiratory horns are absent (character 38) and the rounded spiracular field is without lobes (character 41). This, together with the absence of characters 49 and 50 supports the systematic position of *Neolimnophila* among the



Figs. 119-126. *Austrolimnophila*, larval characters. – 119, *A. ochracea*, head capsule (cs, coronal suture; fs, frontal suture), dorsal view; 120, idem, ventral view; 121, *A. medialis*, left maxilla (mp, maxillary palp), ventral view; 122, *A. ochracea*, hypopharynx (hp), hypopharyngeal bar (hb) and prementum (pm); 123, idem, spiracular disc; 124, idem, hypostoma; 125, idem, right mandible, dorsal view; 126, idem, labrum, dorsal view. – Figs. 127-128. *Dactylolabis*, larval characters. – 127, *D. sexmaculata*, spiracular disc; 128, *D. transversa*, left mandible, dorsal view. – Figs. 129-130. *Epiphragma*, larval characters. – 129 *E. ocellare*, labrum, dorsal view; 130, *E. fasciapenne*, terminal segment, oblique posterior view (figs. 119, 120, 122-125: Lindner 1959; 121, 126: Wood 1952; 127-129: Brindle & Bryce 1960; 130: Alexander & Byers 1981) (all figures redrawn).



Figs. 131-132. *Dicranoptycha pallida*, larval characters. – 131, head capsule, ventral view; 132, hypopharynx and hypopharyngeal bar. – Figs. 133-137. *Helius longirostris*, larval characters. – 133, right maxilla, ventral view; 134, head capsule, dorsal view; 135, hypostoma (ap, apophyse); 136, spiracular disc; 137, larva, lateral view. – Fig. 138, *Limnophilomyia lacteitarisus*, left mandible, dorsal view (figs. 131, 132: Alexander 1919b; 133-137: Cramer 1968; 138: Wood 1952) (all figures redrawn).

Cladurini, although character 53 seems to be present.

Sigmatomera (Eriopterinae). – Hudson (1920) provides information for *Sigmatomera* (*Austrolimnobia*) *rufa*. Larvae are living in the semi-liquid vegetable detritus at the stem of the epiphytic *Astelia* leaves and the pupa is enclosed in an upright, rather tough, extremely elongate silken tube. Alexander (1930) adds interesting notes on the biology of the larva of *Sigmatomera* (*Sigma-*

tomera) *shannoniana*. The larva is predacious and lives in rot holes of trees where it makes permanent slimy galleries in the debris, cementing the particles together with the same slimy substance. The prey are Culicidae larvae, which are tremendously eager to feed on the slimy substance and, while feeding, are devoured by the *Sigmatomera* larva.

The combination of predatory larva and pupa in a silken tube is found only in Pediciini. The larva of *rufa* has dorsal and ventral creeping welts on

segments 5-10 as in *Ula* and several other Tipuloidea, whereas Pediciini have a reduced number of creeping welts (character 84), indicating that *Sigmatomera* represents one of the most basal lineages of the Pediciini.

Teucholabis (Eriopterinae: Cladurini). – In *Teucholabis complexa*, immature stages of which are described and figured by Alexander (1920), the following characters are present: 37 (fig. 52), 42, 49, 50, 53. Not present are: 36, 38 (the respiratory horns are short), 43 and 56. Information about the other characters is not available. *Teucholabis* is usually considered to belong to the Cladurini but the characters of the larva and pupa point in the direction of Eriopterini or Molophilini, in spite of the aberrant three lobed spiracular field.

Trentepoblia (Eriopterinae: Gonomyiini). – The limited amount of information available for *Trentepoblia* is reviewed by Alexander (1920) and points towards a relationships with *Limnophilomyia*. Both genera are usually considered to belong to the Eriopterinae but in fig. 4, *Limnophilomyia* is placed next to the Limoniinae, at about the position suggested by Rogers & Byers (1956). Characters in common in *Trentepoblia* and *Limnophilomyia* are reduction of the spiracular lobes, very elongate anal papillae divided by constrictions (as in several species of *Lipsothrix* (Hynes 1965) and Hexatomiinae, see character 72), inner leg sheaths of the pupa the longest (character 33).

Elephantomyia. – This genus has been placed with a wide array of genera and tribes: in *Limnobia anomala* (Osten Sacken 1869), in Antochini (Alexander 1919a), with *Toxorhina* in the Elephantomyiini as part of the Eriopterinae (Alexander 1920), in Elephantomyiini as part of the Hexatomiinae (Alexander 1927; Savchenko 1983a), in Limnophilini as part of the Hexatomiinae (Savchenko & Krivolutskaja 1976), in Heliini or Elephantomyiini as part of the Limoniinae (Lackschewitz 1932; Lackschewitz & Pagast 1940-1942; Savchenko et al. 1992).

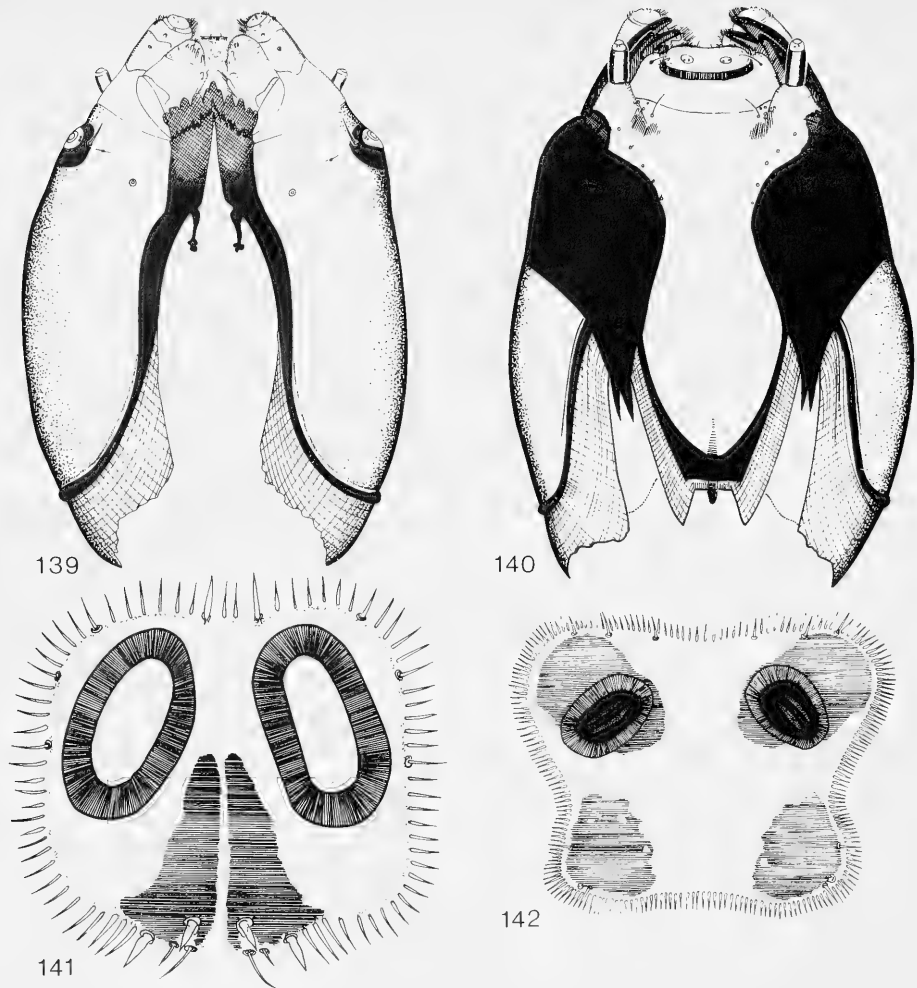
Immature stages of five *Elephantomyia* species are known. Larvae and pupae are described and figured by Alexander (1920) for the type-species *westwoodi*, by Bangerter (1934) for *edwardsi* and by Wood (1952) for *montana* and *aurantiaca*, with the additional note that the pupa of *pseudosimilis* closely resembles that of *montana*.

Elephantomyia is the only genus of Tipuloidea with two strikingly different types of larvae. These differences are coupled with the larval habitat. The species *aurantiaca* and *pseudosimilis* live in moss cushions in waterfalls or along the edges of streams

and tricklets. The larva of *pseudosimilis* is unknown, but the larva of *aurantiaca* has a massive head capsule of 'Limonian construction' (Wood 1952). The larvae of the other three species live in decaying wood. Their head capsule is minute, narrow, consisting of three elongate plates, and very different from the 'Limonian type', or any other type of head capsule. The amount of difference is so large that one is inclined to believe that at least different genera are involved. However, *Elephantomyia* is most probably monophyletic on account of characters of the adults. Furthermore, the four described larva are the only Tipuloidea with creeping welts restricted to sternites 8 to 10.

The three species living in decaying wood (*westwoodi*, *edwardsi* and *montana*), share the following characters: (A.) Body tapering toward either end but more abruptly anteriorly with the head capsule protruding as a sharp narrow point. – (B.) Sternites 8-10 anteriorly with a very conspicuous mouth-like depression. – (C.) Sternite 11 with a transverse mouth, lying near end of segment, its anterior lip with a dense fringe of long hairs directed backward. According to Bangerter (1934) the four delicate anal papillae can be retracted into the opening, to be closed off by the long hairs. – (D.) Spiracular disc surrounded by four lobes (fig. 172). – (E.) Head capsule (fig. 171) very small, narrow and elongate. – (F.) Mandibles very small (see for details Bangerter 1934). – (G.) Mental region feebly chitinated. – (H.) Oesophageal region strengthened with oblique parallel ridges of chitin, producing a latticed effect. – (I.) Antennal papilla large, suboval. – (J.) Sides of head capsule on swelling behind the maxilla with a brush of very long hairs (not certain for *montana*). – (K.) Pupal legsheaths with fore femora distinctly swollen. This last character is mentioned for *montana* by Wood (1952: 247) and it must be assumed that it also present in *pseudosimilis*. The species *westwoodi* and *edwardsi* have the larval thoracic and abdominal segments with a dorsal and ventral transverse ridge of short, stiff hairs just before the caudal margins and a conspicuously elongate bristle on the ventral spiracular lobes (fig. 172).

Of the above mentioned characters, characters D and G are found in other Tipuloidea as well. All other characters are unique and of little help in establishing the phylogenetic position of *Elephantomyia*. On the other hand, all five species have the pupal abdominal segments unarmed (character 14), and *aurantiaca* possesses a massive head capsule with a complete, five-toothed hypostoma (fig. 170, character 11), a toothed prementum (character 16; ventral plate of hypopharynx in Wood 1952) and a reduced spiracular field as in Limoniini (fig. 169, character 104). These characters indicate



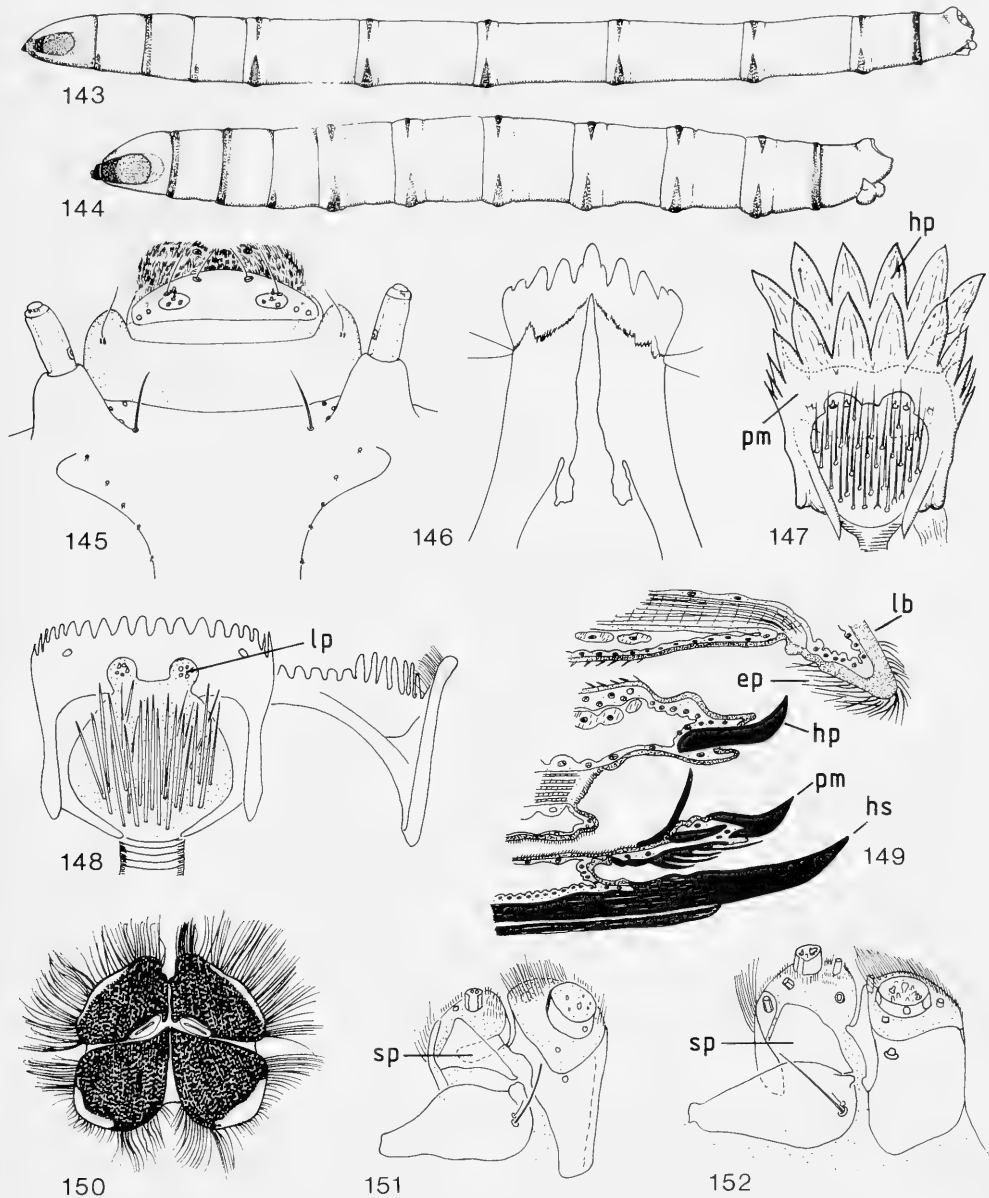
Figs 139-142. Limoniinae, larval characters. – 139, *Limonia macrostigma*, head capsule, ventral view; 140, idem, dorsal view; 141, *Dicranomyia modesta*, spiracular disc; 142, *L. macrostigma*, spiracular disc (Lindner 1959) (figures redrawn).

that at least *aurantiaca*, but probably *Elephantomyia* as a whole, belongs to the Limoniinae. According to Wood (1952), the *aurantiaca* larva has a head capsule resembling that of *Geranomyia sexocellata*, from which it differs only in the armature of the mentum and the antenna.

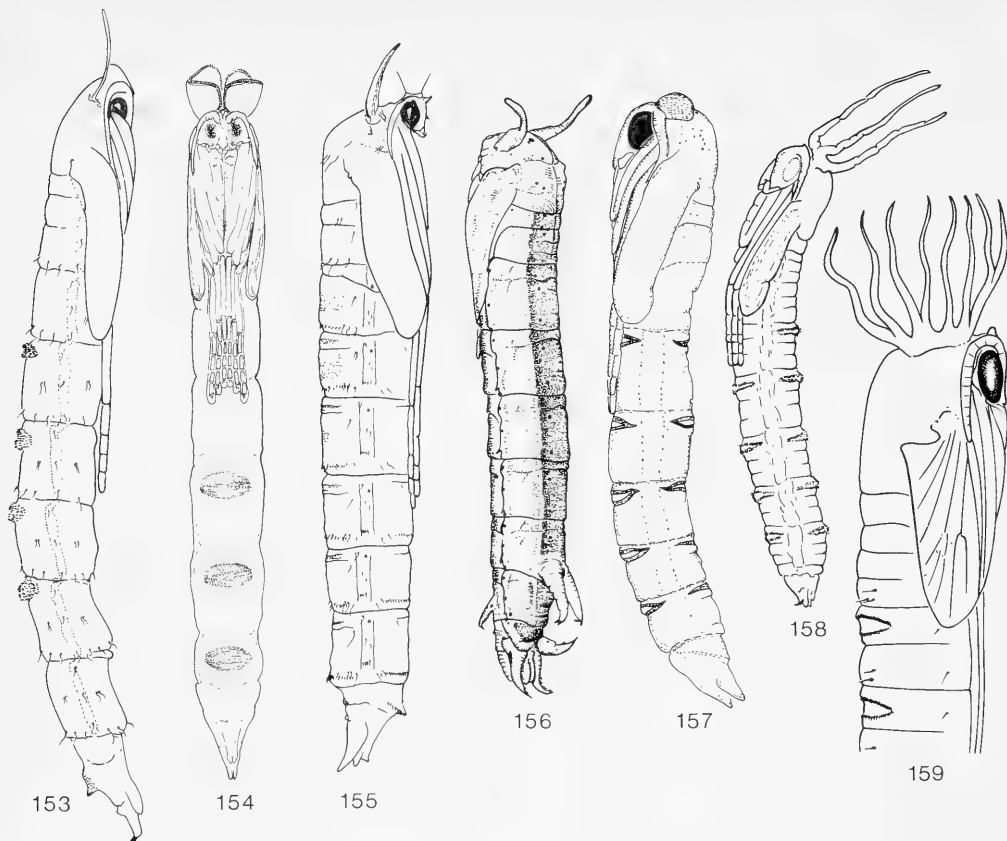
Atarba (Hexatominæ). – Larva and pupa of *Atarba picticornis* are described by Rogers (1927a), who stated that 'on the basis of larva and pupa characters, *Atarba* very clearly is among the genera whose relationships are with the Limoniini [=Limoniinae]'. On adult characters, *Atarba* is generally considered a tribe of its own, placed in the

Hexatominæ (Byers 1981, Savchenko et al. 1992).

Atarba picticornis possesses a complete hypostoma, as found in *Ula* and the *Dactylolabis*-Tipulidae lineage only. Of the characters mentioned in figure 4, no information is available for characters 8, 10, 12, 18, 19 and 35. Of the other characters, 4, 5, 14, 15, 16, probably 17 (interno-lateralia partly fused), 26, 28, 29 and 30 (but segments 3-11 with a unique arrangement of very low creeping welts) and 34 are present. Apart from character 26 (penultimate segment inflated), this strongly indicates that *Atarba* might indeed represent one of the most basal lineages of the Limoniinae, in figure 8 branching of between characters 9 and 99. Charac-



Figs. 143-152. Limoniinae, larval characters. - 143, *Dicranomyia modesta*, larva, lateral view; 144, *Limonia macrostigma*, larva, lateral view; 145, idem, labrum and antennae, dorsal view; 146, idem, hypostoma; 147, *Dicranomyia trifilamentosa*, hypopharyngeal teeth (hp) and prementum (pm), ventral view; 148, *Metalimnobia bifasciata*, prementum, rudimentary labial palps (lp) and part of hypopharynx (displaced laterally), ventral view; 149, *Dicranomyia monostromia*, cross section through anterior part of larval head, showing labrum (lb), epipharynx (ep), hypopharynx (hp), prementum (pm) and hypostoma (hs); 150, *Orimarga mirabilis*, spiracular disc; 151, *Dicranomyia autumnalis*, left maxilla (sp, separate sclerotized plate on inner lobe), ventral view; 152, *D. modesta*, left maxilla (sp, separate sclerotized plate on inner lobe), ventral view (figs. 143-146, 152: Lindner 1959; 147: Tokunaga 1933; 148, 151: Cramer 1968; 149: Tokunaga 1930; 150: Rogers 1927c) (all figures redrawn).



Figs. 153-159. Pupae. - 153, *Limnophilomyia lacteitarus*, female, lateral view; 154, *Lipsothrix sylvia*, female, ventral view; 155, *Austrolimnophila medialis*, female, lateral view; 156, *Phalacrochera replicata*, female, laterodorsal view; 157, *Metalimnobia bifasciata*, female, lateral view; 158, *Dicranomyia trifilamentosa*, female, lateral view; 159, *Antocha saxicola*, female, lateral view (figs. 153, 155: Wood 1952; 154: Rogers & Byers 1956; 156: Peus 1952; 157: Cramer 1968; 158: Tokunaga 1933; 159: Alexander 1920) (all figures redrawn).

ters listed exclusively for the Eriopterinae (fig. 5), Hexatominae (fig. 6), Pediciinae (fig. 7) and Limoniinae (fig. 8) are not present except for character 37 (pupa with middle leg sheaths the shortest).

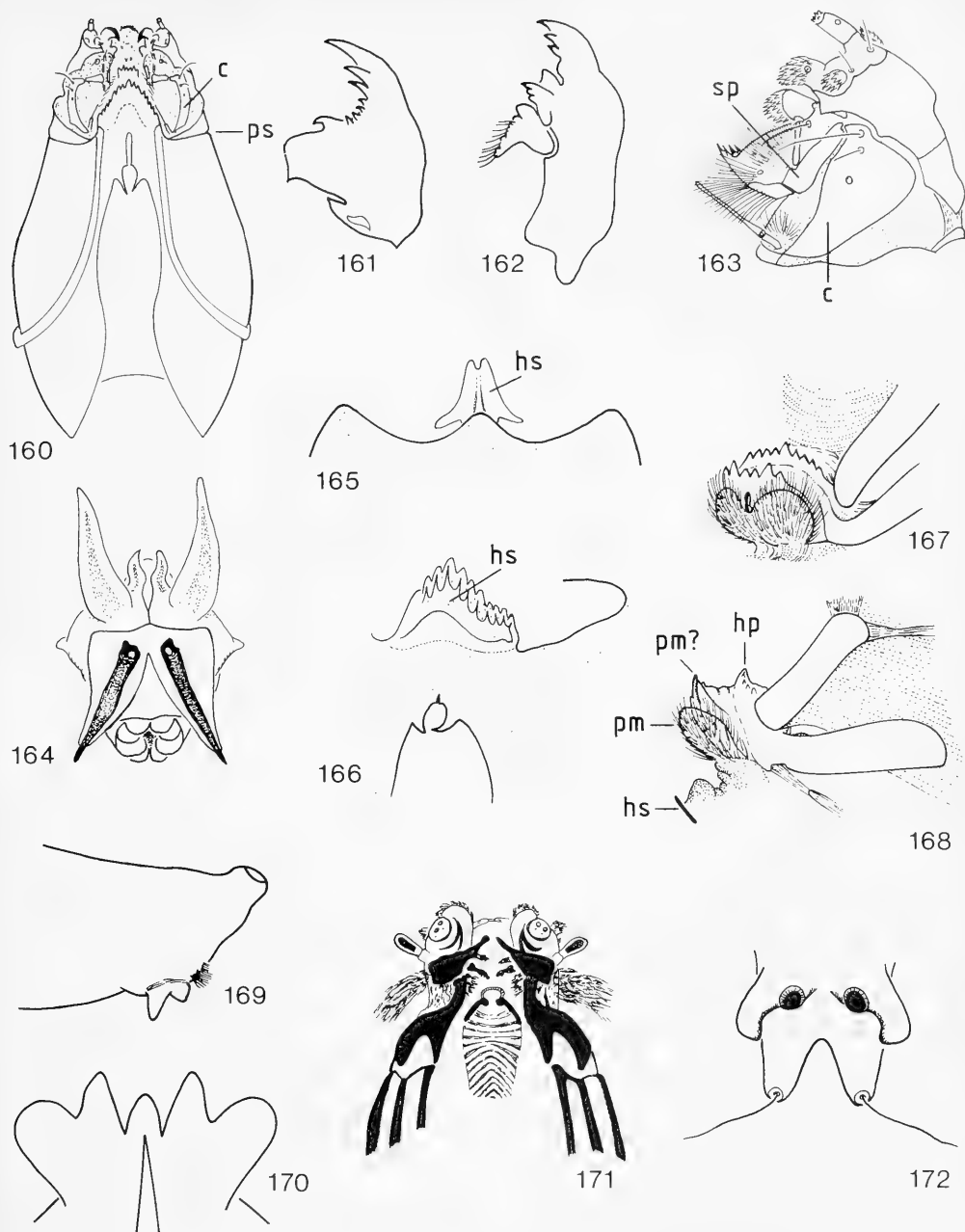
Idioptera, *Rhampophila* and *Tonnoiraptera* (Hexatominae). - The information provided for *Idioptera pulchella* (by Brindle & Bryce 1960, Brindle 1967), *Rhampophila obscuripennis* (by Hudson 1920, as *Limnophila sinistra*) and *Tonnoiraptera neozelandica* (by Tonnoir 1926, as *Alexandrella*) is very limited. According to Brindle & Bryce the larva of *I. pulchella* closely resembles the larva of *Phylidorea*. Typical hexatomine characters are not mentioned for *R. obscuripennis* but seem to be present in *T. neozelandica* (Tonnoir 1926: 'the head armature is typically that of the tribe Hexatomini [=Hexatominae] of the carni-

vorous group, with elongated and very much dissected capsule and with sharp, curved mandibles').

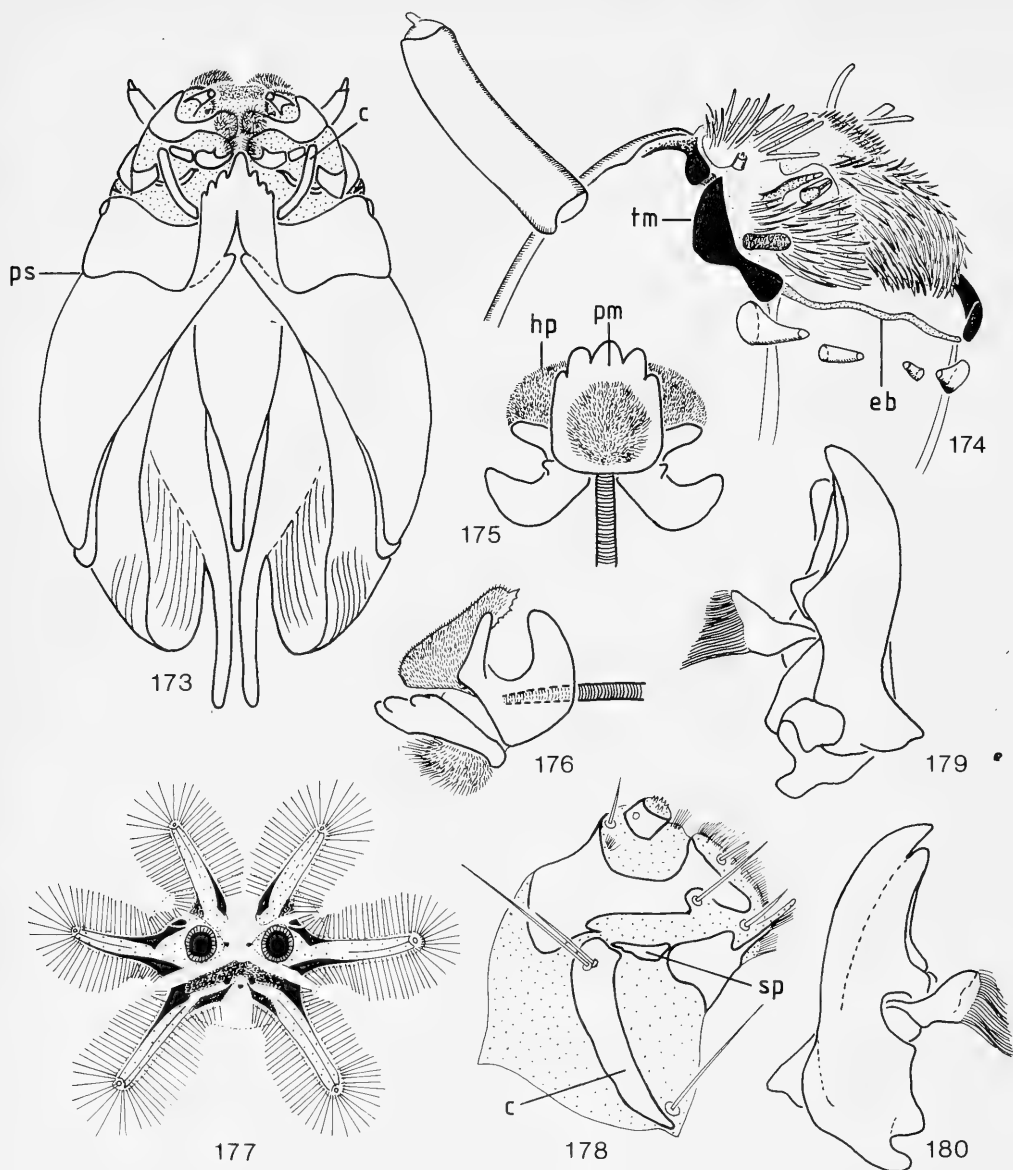
Achyrolimonia and *Neolimonia* (Limoniinae: Limoniini). - The information on the larva of *Neolimonia dumetorum* (Beling 1886) and *Achyrolimonia decemmaculata* (Brindle 1967) shows that characters 101, 102 (spiracles oblong and placed obliquely) and 104 (spiracular lobes reduced) are present. Therefore, both genera are to be placed among the Limoniini.

10. INDEX TO THE LITERATURE

Information from the literature is found in a wide variety of publications and in various forms (notes, descriptions, keys, figures). A number of the more important publications are mentioned in



Figs. 160-168. *Cylindrotominae*, larval characters. – 160, *Phalacrocera replicata*, head capsule (c, cardo; ps, premaxillary suture), ventral view; 161, idem, left mandible of first instar larva, ventral view; 162, idem, right mandible of last instar larva, from inside; 163, idem, left maxilla (c, cardo; sp, separate sclerotized plate on inner lobe), oblique ventral view; 164, *Diogma glabrata*, spiracular field; 165, *P. replicata*, hypostoma (hs) of first instar larva, ventral view; 166, idem, hypostoma (hs) of full grown larva, ventral view; 167, 168, idem, hypopharynx (hp) and prementum (pm), oblique frontal and lateral view. – figs. 169-172. *Elephantomyia*, larval characters: 169, *E. aurantiaca*, abdominal end, lateral view; 170, idem, hypostoma; 171, *E. edwardsi*, anterior part of head capsule, ventral view; 172, *E. westwoodi*, spiracular field (figs. 160, 163, 164, 167, 168: Peus 1952; 161, 162, 165, 166: Bengtsson 1897; 169, 170: Wood 1952; 171: Bangerter 1934; 172: Alexander 1920) (all figures redrawn).



Figs. 173-180. Tipulidae, larval characters. – 173, *Brachypremna dispellens*, head capsule (c, cardo; ps, premaxillary suture), ventral view; 174, *Holorusia* spec. (from Brazil, cf. *juyuyensis*), epipharynx (tm, torma; eb, epipharyngeal bar), lateroventral view; 175, 176, *Tipula livida*, hypopharynx (hp) and prementum (pm), ventral and lateral view; 177, *Prionocera turcica*, spracular disc; 178, *T livida*, right maxilla (c, cardo; sp, separate sclerotized plate on inner lobe), ventral view; 179, 180, *Nephrotoma* spec., left mandible, ventral and dorsal view (fig. 173: Gelhaus & Young 1991; 174: original; 175, 176, 178: Chiswell 1955; 177: Theowald 1957; 179, 180: Savchenko 1983b) (all figures redrawn).

chapter 2. Not all of these publications are indexed here because some of them are compilations only. Genera, subgenera and species are listed alphabetically. An effort has been made to give reference to

all the available literature containing relevant information. The authors are grateful for additions to this index. In the index the following marks are used:

+ Type-species.

V! Preserved material available, Zoological Museum, Amsterdam.

L Larva.

P Pupa.

* Identification of pre-imaginal stages not certain.

Achyrolimonia

decemmaculata Loew: Brindle 1967 (LP), Savchenko 1985 (LP).

Afrolimonia: see under *Libnotes*.

Amalopsis: see under *Pedicia*.

Antocha (Antocha)

bifida Alexander: Hinton 1966, 1968 (P).

monticola Alexander: Needham & Christensen 1927 (LP)

+ *saxicola* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (LP), Peterson 1960 (L), V! (L).

viripennis Meigen: Hinton 1957 (P), Brindle 1967 (LP), Hinton 1968 (P), Rozkosny & Pokorný 1980 (L), Savchenko 1985 (LP), V! (LP).

spec.: Malloch 1917 (L) (as *Genus incertus* 2), Vimmer 1928 (LP, as *calceata*), Alexander 1931 (LP), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L).

Antocha (Orimargula)

+ *alpigena* Mik: Bangertner 1929 (LP), Rozkosny & Pokorný 1980 (L), Savchenko 1985 (LP).

australiensis Alexander: Hinton 1965, 1968 (P).

Aphrophila

neozelandica Edwards: Winterbourn & Gregson 1989 (L).

Arctoconopa

carbonipes Alexander: Hynes 1969a (LP), Byers 1978 (L), Savchenko 1982 (LP).

Atarba

+ *picticornis* Osten Sacken: Rogers 1927a (LP).

viridicolor Alexander: Rogers 1927a (P).

spec.: Byers 1981 (L).

Atypophthalmus

inustus Meigen: Beling 1878 (LP, as *obscuricornis*), V! (P).

+ *umbratus* de Meijere: de Meijere 1917 (L).

Austrolimnobia: see under *Sigmatomera*.

Austrolimnophila

medialis Alexander: Wood 1952 (LP).

ochracea Meigen: Beling 1873a (LP, as *pallida*), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (P).

Baeoura

claripennis Alexander: Wood 1952 (LP).

witzenbergi Wood: Wood 1952 (P).

Brachylimnophila: see under *Neolimnomyia*.

Cheilotrachia (Empeda)

cinerascens Meigen: *Levy 1919 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (L), Krivosheina 1969 (L), Savchenko 1982 (P), 1986 (L), Reusch 1988 (LP).

Chionea

alexandriana Garrett: Byers 1983 (P).

+ *araneoides* Dalman: Egger, Frauenfeld & Brauer 1854 (L), Alexander 1920 (L), Savchenko 1982 (L).

lutescens Lundström: Edwards 1936 (P), Savchenko 1982 (P), Byers 1983 (P).

scita Walker: Byers 1983 (L).

stoneana Alexander: Byers 1983 (L).

Cladura

+ *flavoferruginea* Osten Sacken: Alexander 1920, 1922 (LP).

Conosia

+ *irrorata* Wiedemann: Wood 1952 (LP).

Crunobia: see under *Pedicia*.

Cryptolabis

magnistyla Alexander: Hynes 1963 (LP).

spec.: Byers 1978 (L), Alexander & Byers 1981 (L).

Cylindrotoma

+ *distinctissima distinctissima* Meigen: Lenz 1920b (LP), Haake, 1922 (L), Peus 1952 (LP), Brindle 1967 (LP), Brodo 1967 (LP).

distinctissima americana Coquillett: Cameron 1918 (LP, as *splendens*), Alexander 1920 (LP, as *splendens*).

Dactylolabis

cubitalis Osten Sacken: Alexander 1920 (P), Johannsen 1934 (P).

denticulata Bergroth: Mik 1894 (LP), Alexander 1920 (LP), Vimmer 1925 (LP), Bangertner 1931 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L).

hudsonica Alexander: Sinclair 1988 (LP).

montana Osten Sacken: Sinclair 1988 (LP), V! (LP).

sexmaculata Macquart: Bangertner 1931 (LP), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

transversa Meigen: Bangertner 1931 (LP, as *gracilipes*), Brindle & Bryce 1960 (L), Brindle 1967 (L), Savchenko 1986 (LP).

wodzickii Nowicki: Nowicki 1867 (LP), Alexander 1920 (LP), Lindner 1959 (L).

spec.: Alexander & Byers 1981 (key).

Dicranomyia (Dicranomyia)

autumnalis Staeger: Cramer 1968 (LP), Savchenko 1985 (LP), 1986 (LP).

capicola Alexander: Wood 1952 (LP).

casei Alexander: Williams 1943 (LP).

chorea Meigen: Reusch 1988 (L), V! (P).

didyma Meigen: Engel 1916 (LP, as *trinitata*), Vimmer 1925 (LP, as *trinitata*), Ussing 1929 (LP), Bryce 1957a (L), Brindle 1967 (LP), Savchenko 1985 (LP), V! (P).

floridana Osten Sacken: Rogers 1932 (LP).

frontalis Staeger: Reusch 1988 (LP).

grimshawi Alexander: Williams 1943 (LP).

halobia Tokunaga: Tokunaga 1936 (P).

humidicola Osten Sacken: Alexander 1920 (LP, as *badia*), Johannsen 1934 (P, as *badia*), Byers 1978 (L).

jacobus Alexander: Williams 1943 (LP).

kauaiensis Grimshaw: Swezey 1915 (LP, as *foliocuniculator*).

mariana Seligo: Seligo 1931 (LP).

marmorata Osten Sacken: Saunders 1928 (LP, as *signipennis*).

mitis Meigen: Vaillant 1956 (L), Brindle 1967 (L), Savchenko 1985 (L).

+ *modesta* Meigen: Vimmer 1925 (LP), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (L).

monostromia Tokunaga: Tokunaga 1930 (LP), Kawada 1960 (LP), Hinton 1968 (P).

nigrescens Hutton: Winterbourn & Gregson 1989 (L).

peringueyi Alexander: Wood 1952 (LP).

punctulata De Meijere: Alexander 1931 (LP).

sera Walker: Szadziwski 1979 (LP).

stulta Osten Sacken: Alexander 1920 (LP), Johannsen

- 1934 (L).
tipulipes Karsch: Wood 1952 (LP).
trifilamentosa Alexander: Tokunaga 1933 (LP), Kawada 1960 (LP), Hinton 1968 (P).
ventralis Schummel: Brindle 1967 (LP), Savchenko 1985 (LP).
vicina Macquart: Hemmingsen et al. 1959 (L, as *canariensis*)
- Dicranomyia (Idioglochina)**
 + *marmorata* Osten Sacken: Hinton 1968 (P), Ring 1978 (P).
tokunagana Alexander: Tokunaga 1939 (L, as *gloriosa*).
- Dicranomyia (Idiopyga)**
melleicanda complicata De Meijere: V! (P).
Dicranophragma: see under *Limnophila*.
- Dicranopycha**
megaphallus Alexander: Young 1987 (LP)
minima Alexander: Alexander 1919b (L).
pallida Alexander: Alexander 1919b (LP, as *winemana*).
spec.: Alexander 1920 (LP).
- Dicranota (Dicranota)**
bimaculata Schummel: Miall 1893 (LP), Malloch 1917 (LP), Levy 1919 (LP), Vimmer 1925 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L), Crisp & Lloyd 1954 (L), Brindle 1967 (LP), Reusch 1988 (LP), V! (L).
 + *guerini* Zetterstedt: *Fahy 1972 (L).
spec.: Vimmer 1906 (L), 1925 (P), Malloch 1917 (L), Vimmer 1924 (L, as *Amalopsis*), Miall 1934 (LP), Cook 1949 (L), Savchenko 1986 (L), Reusch 1988 (L), V! (L).
- Dicranota (Paradicranota)**
robusta Lundström: Brindle 1962, 1967 (LP), Savchenko 1986 (LP).
subtilis Loew: Lindner 1959 (L), Brindle 1962, 1967 (L), Savchenko 1986 (L).
- Dicranota (Raphidolabina)**
claripennis Verrall: Brindle 1962, 1967 (L).
 + *flaveola* Osten Sacken: Alexander 1920 (LP).
- Dicranota (Raphidolabis)**
cayuga Alexander: Alexander 1920 (L).
exclusa Walker: Nielsen et al. 1954 (L), Brindle 1962 (L).
 + *tenuipes* Osten Sacken: Needham 1908 (L), Alexander 1920 (L).
- Diogma**
 + *glabrata* Meigen: Muggenberg 1901 (LP), Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Peus 1952 (LP), Brindle 1967 (LP), Krivosheina 1969 (L).
spec.: Malloch 1917 (L), Byers 1978 (L).
Diotrepha: see under *Orimarga*.
- Discobola**
 + *annulata* Linnaeus: Krivosheina 1969 (L), Savchenko 1985, 1986 (L), Krivosheina et al. 1986 (L).
caesaria Osten Sacken: Mik 1884 (P), Alexander 1920 (P).
- Elephantomyia**
aurantiaca Alexander: Wood 1952 (LP).
edwardsi Lackschewitz: Bangerter 1934 (LP), Savchenko 1986 (LP).
montana Alexander: Wood 1952 (LP).
pseudosimilis Alexander: Wood 1952 (P).
 + *westwoodi* Osten Sacken: Alexander 1920 (LP).
spec.: Malloch 1917 (L) (as Genus incertus 1), Krivosheina 1969 (L), Savchenko 1986 (L).
- Elliptera**
 + *omissa* Schiner: Mik 1886 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Vimmer 1925 (L), Bangerter 1934 (LP), Johannsen 1934 (LP), Brindle 1967 (LP), Savchenko 1985 (LP), V! (LP).
- Ellipteroides (Ellipteroides)**
lateralis Macquart: Bangerter 1928 (LP), Brindle 1967 (LP), Savchenko 1982 (LP).
Ellipteroides (Progonomyia)
nigrobimbo Alexander: Wood 1952 (LP).
Ellipteroides (Protogonomyia)
alboscuteclatus von Roser: Bangerter 1930 (LP), Brindle 1967 (LP), Savchenko 1982 (LP).
- Eloeophila (= Ephelia)**
apicata Loew: Brindle & Bryce 1960 (L), Brindle 1967 (LP).
debiosa Alexander: Wood 1952 (LP).
 + *maculata* Meigen (= *marmorata* Meigen): Wolff 1922 (L), Bangerter 1928 (LP), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Pokorny 1978 (LP), Savchenko 1986 (LP), Reusch 1988 (P), V! (L).
mundata Loew: Brindle & Bryce 1960 (L), Pokorny 1978 (LP), Savchenko 1986 (LP).
submarmorata Verrall: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Pokorny 1978 (LP), Savchenko 1986 (LP).
trimaculata Zetterstedt: Brindle & Bryce 1960 (L), Brindle 1967 (LP).
verralli Bergroth: Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Reusch 1988 (P).
spec.: Walton 1944 (L, as undescribed, erroneously considered *Pedicia rivosia* by Hinton 1950), Alexander & Byers 1981 (L, as *Limnophila spec.*), V! (L).
- Elporiomyia*: see under *Limnophila*.
Empeda: see under *Cheilotrichia*.
- Epiphragma**
 + *fasciapenne* Say: Needham 1903, 1908 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Teskey 1976 (L), Alexander & Byers 1981 (L).
imitans Alexander: Bruch 1939 (LP).
ocellare Linnaeus: Beling 1873b (LP, as *picta*), *Wolff 1922 (L, as *punctata*), Vimmer 1925 (LP, as *punctata*), Hennig 1950 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Krivosheina 1969 (L), Mamaev et al. 1977 (L), Savchenko 1986 (LP), V! (P).
solatrix Osten Sacken: Alexander 1920 (LP).
spec.: Crisp & Lloyd 1954 (L). *Eriocera*: see under *Hexatoma*.
- Eriocnopa**
 + *trivialis* Meigen: Nielsen et al. 1954 (L), Okely 1979 (LP), Savchenko 1986 (L), V! (L).
- Erioptera (Erioptera)**
chlorophylla Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (LP).
cladophoroides Alexander: Bruch 1939 (LP).
fusculeta Edwards: Brindle 1967 (LP), Savchenko 1982 (P).
flavata Westhoff: Beling 1878 (LP, as *flavescens*), Vimmer 1925 (LP, as *flavescens*), Brindle 1967 (LP, as *flavescens*), Savchenko 1986 (L, as *geminata*).
 + *lutea* Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Bangerter 1930 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1982 (L), Reusch 1988 (P).
megophthalma Alexander: Alexander 1920 (LP).

- septemtrionis* Osten Sacken: Alexander 1920 (P).
squalida Loew: Houlihan 1969 (P).
vespertina Osten Sacken: Alexander 1920 (P).
spec.: *Dette 1916 (L, as *flavescens*) *Keilin 1944 (L), Peterson 1960 (L), V! (L).
- Erioptera (Mesocyphona)**
spec.: Alexander 1920 (P).
- Eugnomyia**
+ *luctuosa* Osten Sacken: Rogers 1928 (LP).
- Euphyllidorea**
lineola Meigen: Beling 1886 (L), Levy 1919 (LP), Vimmer 1925 (LP), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L).
meigenii Verrall: Nielsen et al. 1954 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L), V! (L).
- Eutonia**
+ *barbipes* Meigen: Wolff 1922 (L).
marchandi Alexander: Hynes 1958 (LP).
spec.: *Hennig 1950 (L, as *Limnophila* spec.).
- Geranomyia**
argentina De Meijere: Alexander 1931 (P).
bezzii Alexander & Leonard: Seurat 1924 (LP).
caloptera Mik: Bangerter 1929 (LP, as *maculipennis*).
canadensis Westwood: Alexander 1920 (LP), Alexander & Malloch 1920 (LP), Johannsen 1934 (LP).
fletcheri Edwards: Alexander 1931 (LP).
gelatifex Edwards: Hingston 1932 (P), Edwards 1934 (P).
rostrata Say: Rogers 1927d (LP), Johannsen 1934 (L), Peterson 1960 (L), Byers 1978 (L).
rubrithorax Alexander: Wood 1952 (LP).
sexocellata Alexander: Wood 1952 (LP).
+ *unicolor* Haliday: Pierre 1926 (LP), Saunders 1930 (LP), Poisson 1932 (LP), Brindle 1967 (LP), Toye 1967 (L), Hinton 1968 (P).
- Gnophomyia**
jacobsoni Alexander: Rogers 1927b (LP), 1928 (L).
lugubris Zetterstedt: Brindle 1967 (LP), Mamaev et al. 1977 (L, as *tristis*), Savchenko 1982 (LP).
toschiae Alexander: Teskey 1976 (L), Alexander & Byers 1981 (L).
+ *tristissima* Osten Sacken: Malloch 1917 (LP), Alexander 1920 (LP), Rogers 1928 (LP).
spec.: Savchenko 1986 (L).
- Gonempeda**
+ *flava* Schummel: Brindle 1967 (P), Savchenko 1982 (P).
- Gonomyia (Gonomyia)**
kansensis Alexander: Alexander 1920 (P).
lucidula De Meijere: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko, 1982 (LP).
spec.: Vimmer 1925 (L), Alexander 1931 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L).
- Gonomyia (Lipophleps)**
hawaiiensis Alexander: *Williams 1943 (L).
pleuralis Williston: Rogers 1926 (LP).
sulphurella Osten Sacken: Alexander 1920 (P), Johannsen 1934 (P).
sulphurelloides Alexander: Wood 1952 (LP).
spec.: Alexander 1931 (L).
- Gonomyia (Neolipophleps)**
alexanderi Johnson: Alexander 1920 (LP).
- Gonomyodes**
tacoma Alexander: Hynes 1969b (LP), Byers 1978 (L).
- Helius**
flavipes Macquart: Alexander 1920 (LP), Johannsen 1934 (P).
flavus Walker: Brindle 1967 (L).
+ *longirostris* Meigen: Gercke 1884 (P), Bangerter 1929 (LP), Brindle 1967 (LP), Cramer 1968 (LP), Savchenko 1986 (LP), Reusch 1988 (L).
mainensis Alexander: Alexander 1920 (LP), Johannsen 1934 (L).
pallirostris Edwards: Brindle 1967 (L).
spec.: V! (L).
- Hesperoconopa**
dolichophallus Alexander: Hynes 1968 (LP).
- Hexatoma (Eriocera)**
albittarsis Osten Sacken: Alexander 1915b, 1920 (LP), Johannsen 1934 (LP).
cinerea Alexander: Alexander 1920 (LP), Johannsen 1934 (LP).
fultonensis Alexander: Alexander 1914a, 1920 (LP), Johannsen 1934 (L), Peterson 1960 (L).
longicornis Walker: Alexander 1914a, 1920 (LP).
spinosa Osten Sacken: Alexander 1914a, 1920 (LP), Johannsen 1934 (L), Peterson 1960 (L), Byers 1978 (L).
spec.: Malloch 1917 (L), Alexander 1931 (L), Cook 1949 (L), V! (L).
- Hexatoma (Hexatoma)**
bicolor Curtis: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (L).
fuscipennis Curtis: Brindle & Bryce 1960 (L), Brindle 1967 (LP), V! (L).
megacera Osten Sacken: Alexander 1915b (LP), 1920 (LP), Johannsen 1934 (LP), Byers 1978 (L).
+ *nigra* Latreille: *Lindner 1959 (L).
spec.: *Wolff 1922 (L, as *Limnophila* spec.; L, as cf *tenuipes*), Rozkosny & Pokorny 1980 (L).
- Hoplolabis (Hoplolabis)**
+ *armata* Osten Sacken: Alexander 1920 (P).
- Hoplolabis (Parilisia)**
vicina Tonnoir: Brindle 1967 (LP), Savchenko 1982 (LP), Reusch 1988 (P).
- Idioglochina*: see under *Dicranomyia*.
- Idioglyphomyia**
enneki Alexander: Byers 1974 (LP).
- Idioptera**
+ *pulchella* Meigen: Brindle & Bryce 1960 (L), Brindle 1967 (L), Savchenko 1986 (L).
- Idiopyga*: see under *Dicranomyia*.
- Ilisia**
+ *maculata* Meigen: Crisp & Lloyd 1954 (L), Brindle 1967 (LP), Savchenko 1982 (L).
- Lasiomastix*: see under *Limnophila*.
- Libnotes (Afrilominia)**
ladogensis Lackschewitz: Savchenko 1985, 1986 (L).
stantoni Edwards: *Alexander 1931 (LP).
subapicalis Alexander: Wood 1952 (LP).
spec.: Savchenko 1986 (L).
- Libnotes (Libnotes)**
perkinsi Grimshaw: Williams 1943 (LP).
undulata Matsumura: Krivosheina 1969 (L), Mamaev et al. 1977 (L).
- Limnophila (Dicranophragma)**
+ *fuscovaria* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L P).
- Limnophila (Elporiomyia)**
crepuscula Wood: Wood 1952 (LP).

+ *nox* Alexander: Wood 1952 (LP).

Limnophila (Lasiomastix)

+ *macrocera* Say: Alexander 1920 (LP), Johannsen 1934 (LP), Byers 1978 (L).

Limnophila (Limnophila) (= Poecilostola)

+ *picipennis* Meigen: Beling 1878 (LP), Brauer 1883 (L), V! (LP).

punctata Schrank: Beling 1886 (LP), Gerbig 1913 (L), Wolff 1922 (L), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorný 1980 (L), Savchenko 1986 (LP).

spec.: Levy 1919 (LP), *Wolff 1922 (L, as *spec.* (= *Hexatoma* ?), as *rufibasis*), Hennig 1950 (L) (= *Eutonia* ?), Lindner 1959 (L), Byers 1978 (L), Savchenko 1986 (L).

Limnophilomyia

+ *lacteitarsis* Alexander: Wood 1952 (LP).

Limonia

flavipes Fabricius: Beling 1886 (L), Brindle 1967 (LP), Reusch 1988 (LP).

hercegovinae Strobl: Reusch 1988 (L).

macrostigma Schummel: Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

nigropunctata Schummel: Beling 1878 (L).

nubeculosa Meigen: Bryce 1957a (L), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

simulans Walker: Needham 1908 (LP), Malloch 1917 (L), Alexander 1920 (LP).

+ *tripunctata* Fabricius: Beling 1873b (LP), Lindner 1959 (L), Brindle 1967 (LP), Savchenko 1985, 1986 (LP), Reusch 1988 (LP).

trivittata Schummel: V! (L).

spec.: Teskey 1976 (L), Byers 1978 (L), Alexander & Byers 1981 (L).

Liogma

+ *nodicornis* Osten Sacken: Alexander 1914b, 1920 (LP), Peus 1952 (LP), Brodo 1967 (LP), Alexander & Byers 1981 (L).

Lipophleps: see under *Gonomyia*

Lipsothrix

errans Walker: Beling 1886 (LP, as *icterica*), Brindle 1967 (LP), Krivosheina 1969 (L), Savchenko 1982, 1986 (LP).

fenderi Alexander: Hynes 1965 (LP).

hynesiana Alexander: Hynes 1965 (LP).

nigrilinea Doane: Hynes 1965 (LP).

remota Walker: Hinton 1955 (P), Brindle 1967 (LP), Hinton 1967, 1968 (P).

shasta Alexander: Hynes 1965 (LP).

sylvia Alexander: Rogers & Byers 1956 (LP), Hynes 1965 (LP).

Mesocyphona: see under *Erioptera*.

Metalimnobia

annulus cinctipes Say: Alexander 1920 (LP).

bifasciata Schrank: Stannius 1829 (LP, as *xanthoptera*), Pastejrik 1908 (L, as *xanthophora*), Vimmer 1912, 1925 (L, as *xanthophora*), de Meijere 1917 (LP), Brauns 1954b (P), Brindle 1967 (LP), Cramer 1968 (L), Savchenko 1985 (LP), 1986 (LP), V! (LP).

fallax Johnson: Alexander 1920 (LP), Johannsen 1934 (LP).

immatura Osten Sacken: Malloch 1917 (P).

quadrinaculata Linnaeus: Beling 1873b (LP, as *annulus*), Brauns 1954b (P), Lindner 1959 (L), Brindle 1967

(LP), Krivosheina 1969 (L), Savchenko 1985, 1986 (L), V! (P).

quadrinotata Meigen: Lindner 1958 (LP), Brindle 1967 (LP), Savchenko 1985 (LP).

tricolleata Osten Sacken: Johnson 1906 (LP), Malloch 1917 (LP).

Molophilus

griseus Meigen: Crisp & Lloyd 1954 (L), Gachet 1967 (LP, as *ripiculus*), Savchenko 1982 (L).

hirtipennis Osten Sacken: Alexander 1920 (LP), Byers 1978 (L).

obscurus Meigen: Brindle 1967 (LP), Savchenko 1982 (P).

occultus De Meijere: Okely 1979 (L), Savchenko 1986 (L).

ochraceus Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Brauns 1954b (P), Reusch 1988 (LP).

spec.: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1986 (L), Winterbourn & Gregson 1989 (L).

Mongoma: see under *Trentepoblia*.

Neolimnomyia (Brachylimnophila)

memoralis Meigen: Beling 1886 (LP), Vimmer 1925 (LP), Crisp & Lloyd 1954 (L), Brindle 1958 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

Neolimnomyia (Neolimnomyia)

batava Edwards: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), Reusch 1988 (P).

filata Walker: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP).

Neolimnophila

carteri Tonnoir: Beling 1886 (LP, as *hyalipennis*).

Neolimonia

dumetorum Meigen: Beling 1886 (L).

Neolipophleps: see under *Gonomyia*.

Orimarga (Diotrepha)

+ *mirabilis* Osten Sacken: Rogers 1927c (LP).

Orimarga

attenuata Walker: Vaillant 1951 (LP, as *hygroptetrica*), Savchenko 1985 (LP).

Orimargula: see under *Antocha*.

hederae Curtis: V! (P).

lineata Meigen: Lindner 1959 (L), Brindle 1967 (L), Savchenko 1982, 1986 (L).

meigenii Osten Sacken: Alexander 1920 (LP), Byers 1978 (L).

nigripila Osten Sacken: Alexander 1920 (P).

romanovichiana Alexander: Alexander 1920 (LP, as *nubila*).

spec.: Johannsen 1934 (L), Byers 1978 (L), Alexander & Byers 1981 (L), Savchenko 1982 (LP), Reusch 1988 (P).

Oxyrhiza: see under *Paradelphomyia*.

Paradelphomyia (Oxyrhiza) (= Oxydiscus).

americana Alexander: *Alexander 1920 (L).

cayuga Alexander: *Alexander 1920 (L).

minuta Alexander: *Alexander 1920 (LP), Johannsen 1934 (L), Savchenko 1986 (P).

senilis Haliday: Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (L), Krivosheina 1969 (L), Savchenko 1986 (L), Reusch 1988 (P).

spec.: Brindle & Bryce 1960 (L).

Paradicranota: see under *Dicranota*.

Paralimnophila

skusei Hutton: Winterbourn & Gregson 1989 (L).

Paramongoma: see under *Trentepohlia*.

Paraphylidorea: see under *Phylidorea*.

Parilisia: see under *Ilisia*.

Pedicia (Amalopsis)

+ *occulta* Meigen: Lindner 1959 (L), Brindle 1967 (L), Savchenko 1986 (L).

Pedicia (Crunobia)

littoralis Meigen: Brindle 1967 (L).

+ *straminea* Meigen: Beling 1878 (LP, as *schineri*), Vimmer 1925 (LP, as *schineri*), Lindner 1959 (L), Brindle 1967 (L), Savchenko 1986 (L).

spec.: Brindle 1962 (L).

Pedicia (Pedicia)

albivitta Walker: Needham 1903 (L, as unidentified), 1908 (L), Alexander 1920 (L), Johannsen 1934 (L), Byers 1978 (L).

+ *rivosa* Linnaeus: Beling 1878 (LP), Levy 1919 (LP), Vimmer 1925 (LP), Oldham 1926 (L), Wardle 1926 (L), Wardle & Taylor 1926 (L), Wesenberg-Lund 1943 (L), Hennig 1950 (L), Brauns 1954b (P), Crisp & Lloyd 1954 (L), Brindle 1962 (L), 1967 (LP), Savchenko 1986 (LP), V! (LP).

spec.: Alexander & Byers 1981 (L).

Phalacrocer

+ *replicata* Linnaeus: Bengtsson 1897 (L), Miall & Shelford 1897 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Johannsen 1934 (LP), Wesenberg-Lund 1943 (L), Peus 1952 (LP), Brindle 1967 (LP), Brodo 1967 (LP), Krivosheina 1969 (L), Byers 1978 (L), V! (L).

tipulina Osten Sacken: Brodo 1967 (P).

vancouverensis Alexander: Spencer 1930 (LP).

Phylidorea (Macrolabina)

+ *nigronotata* Siebke: Wiedenska 1987 (LP).

Phylidorea (Paraphylidorea)

+ *fulvonervosa* Schummel: Crisp & Lloyd 1954 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (L), Wiedenska 1987 (LP), Reusch 1988 (P).

Phylidorea (Phylidorea)

abdominalis Staeger: Brindle 1967 (LP).

adusta Osten Sacken: *Alexander 1920 (LP), Johannsen 1934 (P).

+ *ferruginea* Meigen: Beling 1878 (P, as *lineola*), de Meijere 1917 (LP), *Levy 1919 (LP), Wolff 1922 (L), Hennig 1950 (P), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), V! (P).

longicornis Schummel: Brindle 1967 (P, as *glabricula*).

nervosa Schummel: Wiedenska 1987 (LP).

squalens Zetterstedt: Brindle & Bryce 1960 (L), Brindle 1967 (LP), Savchenko 1986 (LP), Wiedenska 1987 (LP).

Pilaria

discicollis Meigen: Gerbig 1913 (L), Levy 1919 (LP), Vimmer 1924, 1925 (P), Brindle 1958 (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorny 1980 (L), Savchenko 1986 (LP), Reusch 1988 (LP), V! (L).

fuscipennis Meigen: Brauer 1883 (L), Beling 1886 (LP), Vimmer 1906 (L), Gerbig 1913 (L), Levy 1919 (LP), Wolff 1922 (L), Vimmer 1925 (LP), Rozkosny & Pokorny 1980 (L), V! (L).

quadrata Osten Sacken: Alexander 1920 (P).

recondita Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L), Alexander & Byers 1981 (L).

ripicola Gérard: Gérard 1968 (LP).

scutellata Staeger: Brindle & Bryce 1960 (L), Brindle 1967 (LP).

tenuipes Say: Malloch 1917 (L), Alexander 1920 (LP), Johannsen 1934 (LP).

spec.: Anton 1943a (L, as ? *Ulomorpha*), Hennig 1950 (L, as ? *Ulomorpha*), Crisp & Lloyd 1954 (L), Byers 1978 (L).

Polymera

georgiae Alexander: Rogers 1933 (LP).

rogersiana Alexander: Rogers 1933 (LP).

Progonomyia: see under *Ellipteroides*.

Protogonomyia: see under *Ellipteroides*.

Pseudolimnophila

inornata Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (P), Byers 1978 (L), Alexander & Byers 1981 (L).

lucorum Meigen: Crisp & Lloyd 1954 (L), Hinton 1954 (P), Brindle 1958 (L), Brindle & Bryce 1960 (L), Brindle 1967 (LP), Rozkosny & Pokorny 1980 (L), Savchenko 1986 (LP), Reusch 1988 (P).

+ *luteipennis* Osten Sacken: Hart 1895 (LP), Malloch 1917 (LP), Alexander 1920 (LP), Johannsen 1934 (L), V! (L).

Psiloconopa: see under *Symplecta*.

Rhabdomastix (Sacandaga)

afra Wood: Wood 1952 (LP).

californiensis Alexander: Hynes 1969c (LP).

fascigera Alexander: Hynes 1969c (LP).

flaviventris Alexander: Hynes 1969c (LP).

hynesi Alexander: Hynes 1969c (LP).

leonardi Alexander: Hynes 1969c (LP).

schistacea Schummel: Beling 1886 (LP), Vimmer 1925 (LP).

setigera Alexander: Hynes 1969c (LP), Byers 1978 (L).

subfascigera Alexander: Hynes 1969c (LP).

trichophora Alexander: Hynes 1969c (LP).

spec.: Savchenko 1982 (LP).

Rhamphophila

+ *obscuripennis* Hudson: Hudson 1920 (LP, sinistra).

Rhaphidolabina: see under *Dicranota*.

Rhaphidolabis: see under *Dicranota*.

Rhipidia

bryanti Johnson: Alexander 1920 (LP), Johannsen 1934 (LP).

+ *maculata* Meigen (= *duplicata* authors): Beling 1873b (P), 1878 (L), Brauns 1954b (P), Brindle 1967 (L), Savchenko 1985 (L), Reusch 1988 (LP).

uniseriata Schiner: Beling 1878 (L).

Rhypholophus

haemorrhoidalis Zetterstedt: Beling 1878 (P), 1886 (LP), Crisp & Lloyd 1954 (L), Lindner 1959 (L), Brindle 1967 (LP), Krivosheina 1969 (L), Savchenko 1982, 1986 (LP), V! (P).

varius Meigen: de Meijere 1917 (LP), Wolff 1922 (L), Brindle 1967 (L P).

spec.: V! (LP).

Sacandaga: see under *Rhabdomastix*.

Scleroprocta

innocens Osten Sacken: Alexander, 1920 (P), Johannsen 1934 (P), Brindle 1967 (P).

+ *sororcula* Zetterstedt: Brindle 1967 (LP, as *danica*), *spec.*: Alexander 1920: Figs 405-406 (as unidentified), Bangert 1930 (LP, as *fascipennis*), Savchenko 1982 (LP).

- Sigmatomera** (Austrolimnobia)
rufa Hudson: Hudson 1920 (LP).
Sigmatomera (Sigmatomera)
shannoniana Alexander: Alexander 1930 (L).
Styringomyia
ingrami Edwards: Edwards 1924 (P).
neocaledoniae Alexander: Hynes 1990 (LP).
Symplecta (Psiloconopa)
graphica Osten Sacken: Hart 1895 (L).
stictica Meigen: Brindle 1967 (LP), Houlihan 1969 (P), Reusch 1988 (LP).
Symplecta (Symplecta)
cana Walker: Hart 1895 (LP, as *punctipennis*), *Malloch 1917 (LP, as *punctipennis*), Vimmer 1925 (LP, as *punctipennis*).
+ *hybrida* Meigen: Beling 1878 (LP, as *punctipennis*), Alexander 1920 (LP), Johannsen 1934 (LP), Savchenko, 1982 (LP), Reusch 1988 (LP), V! (L).
macroptera Philippi: Bruch 1939 (LP).
Symplecta (Trimicra)
+ *pilipes* Fabricius: Beling 1878 (LP), Gerbig 1913 (L), Alexander 1920 (L), Pierre 1924 (P, as *marina*), Vimmer 1925 (LP), Johannsen 1934 (L), Bruch 1939 (LP), Séguy 1942 (LP, as *pauliana*), Wood 1952 (LP, as *inconspicua*), Vaillant 1953 (LP, as *hirsutipes*), Brindle 1967 (L), Byers 1978 (L), Savchenko 1982 (L).
Teucholabis
+ *complexa* Osten Sacken: Alexander 1920 (LP).
Thaumastoptera
+ *calceata* Mik: Lenz 1920a (LP), Liang 1925 (LP), Brauns 1954b (P), Vaillant 1956 (L), Brindle 1967 (LP), Savchenko 1985 (LP).
spec.: Vimmer 1929 (L).
Tonnoiraptera
+ *neozelandica* Tonnoir: Tonnoir 1926 (P).
Trentepohlia (Mongoma)
pennipes Osten Sacken: de Meijere 1911 (LP), Alexander 1920 (LP).
Trentepohlia (Paramongoma)
bromeliadicola Alexander: Picado 1913 (LP), Alexander 1920 (LP).
Triclyphona
+ *immaculata* Meigen: Beling 1878 (L), de Meijere 1917 (LP), Lindner 1959 (L), Brindle 1962 (L), 1967 (LP), Okely 1979 (L), Savchenko 1986 (LP).
inconstans Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L), Byers 1978 (L).
schummeli Edwards: Brindle 1967 (L).
unicolor Schummel: Brindle 1962 (L), 1967 (LP).
Trimicra: see under *Symplecta*.
Triogma
exsculpta Osten Sacken: Brodo 1967 (LP).
+ *trisulcata* Schummel: Alexander 1920 (LP), Lenz 1920b (LP), Haake 1922 (LP), Johannsen 1934 (L), Wesenberg-Lund 1943 (L), Peus 1952 (LP), Brindle 1967 (LP), V! (L).
Ula
bolitophila Loew: Krivosheina 1969 (L), Krivosheina et al. 1986 (L), Savchenko 1986 (L).
elegans Osten Sacken: Alexander 1915a (LP), Malloch 1917 (LP), Alexander 1920 (LP).
+ *mollissima* Haliday: Engel 1916 (L, as *macroptera*), Vimmer 1925 (LP, as *macroptera*), Lindner 1959 (L, as *crassicauda*), Savchenko 1986 (L).
sylvatica Meigen: Bangerter 1934 (LP), Bryce 1957b (L), Lindner 1959 (L), Brindle & Bryce 1960 (L), Brin-

- dle 1967 (LP), Savchenko 1986 (LP), V! (LP).
- Immature stages of Japanese *Ula* species are described by Tokunaga et al. 1954 (not consulted).
Ulomorpha
+ *pilosella* Osten Sacken: Alexander 1920 (LP), Johannsen 1934 (L).
spec.: Anthon 1943a (L), Hennig 1950 (L).

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BOOK REVIEW

Moller Pillot, H. K. M. & R. F. M. Buskens, 1990. De larven der Nederlandse Chironomidae (Diptera). Deel C: Autoecologie en verspreiding. [The larvae of the Dutch Chironomidae (Diptera). Part C: Autecology and distribution]—Nederlandse Faunistische Mededelingen 1C: 1-87, figs 1-2, tables 1-5, maps 1-182. [Stichting European Invertebrate Survey—Nederland; send orders to 'The Library, Nationaal Natuurhistorisch Museum, P.O. Box 9517, 2300 RA Leiden, Nederland'. Price 20 Dutch Guilders. Price of parts 1A-C together 100 Dutch Guilders. Text in Dutch, but an explanation in English of the table containing all ecological information is available on request].

Keys for the identification of larvae of Dutch Chironomidae by H. Moller Pillot were published in the series Nederlandse Faunistische Mededelingen (parts 1A and 1B) in 1978 and 1984. In both works keys are given for the majority of genera, but the identification of species appeared to be difficult or impossible in many cases. For this reason Moller Pillot introduced a system of species-groups, aggregates, and sometimes even artificial names, e.g. '*Chaetocladius* spec. Herkenbosch', for larvae that could clearly be recognised although no unequivocal correlation could be made with species already described as adults. Thus a system of about 200 larval taxa was created, covering all Chironomidae, except for the Tanytarsini.

Chironomidae have proved to be good indicators to various conditions of the aquatic and semi-aquatic environment. For this reason they play an important role in several systems for the biological assessment of water quality. As these systems came into use on a wide scale throughout The Netherlands during the eighties, the keys by Moller Pillot were widely used soon after publication. New water quality systems were developed as well, in which the taxa of Moller Pillot were incorporated.

Already from the beginning of his studies on Chironomidae, Moller Pillot collected ecological data from his own investigations as well as data coming forth from the use of the keys in combination to large environmental research projects and the systems for the biological assessment of water quality. Dozens of students from all over The Netherlands put their data to disposal. Based on these data, Moller Pillot and Buskens have now prepared the third and final part (part 1C) of the work on Dutch Chironomidae.

The book deals with the autecology and the geographic distribution of the ca. 200 taxa distinguished in parts 1A and 1B. The nomenclature from parts 1A and 1B has been maintained as much as possible; a brief list on page 78 in part 1C indicates the names that had to be changed or were added since.

The autecology is summarized in a brief but elegant way. In a large table, which represents the most important part of the book, the ecological response of all taxa to a number of environmental factors is given. Factors treated in the table are water type, habitat, oxygen, chloride concentration and the acidity in combination with the trophic level. Each factor is split up in a number of conditions. The ecological response of each taxon for each condition of each factor is roughly indicated on a scale, varying between 0 and 4. These numbers indicate the relative abundance of the taxa under the conditions mentioned, in a range from total absence to a high abundance.

The authors emphasize that habitat preference of species is often not determined by the mean values of environmental factors, but by critical values instead. For instance, four conditions of the factor oxygen are given in the table: stable (saturation always more than 50%), instable (saturation level between 10 and 50% at least once a day), saturation level below 5% for at most a few hours a day, and saturation level below 5% for many hours each day in summer. This approach offers more adequate ecological information than a given response to mean oxygen values would do.

Additional information for each taxon is given in a series of short notes, concerning the life cycle and ecological details not mentioned in the large table. In a number of cases the distribution patterns of taxa are discussed from an ecological point of view.

The distribution patterns in The Netherlands are represented by 182 maps, using the 10 km UTM-grid. Only records checked by the authors were included in these maps. For a better understanding of the distribution patterns maps of the distribution of soil types and brackish water in The Netherlands were added. In addition to the maps, the species abundance is mentioned in the large table as well, giving the number of 10 km squares from the maps and by using a code for the number of 5 km squares from the Dutch National Grid.

The parts A, B and C together reflect the results of many years of investigations and all data presented are original. This is not only important from a scientific point of view. Especially the suitability for practical use, of which an example is worked out in part C, makes the work most valuable. Although the text is in Dutch, the books are of importance for chironomid workers outside The Netherlands as well. The keys (parts A and B) contain figures of relevant parts of the body of all taxa included, while the data on the ecology and distribution (in part C) are readily accessible by the concise way of presentation.

[A. W. M. Mol]

REVIEW OF THE ORIENTAL GENUS *ANGERIANUS* DISTANT (HETEROPTERA: MIRIDAE)

Stonedahl, G. M., 1991. Review of the Oriental genus *Angerianus* Distant (Heteroptera: Miridae). – *Tijdschrift voor Entomologie* 134: 269-277, figs. 1-20. [ISSN 0040-7496]. Published 18 December 1991.

The genus *Angerianus* Distant is diagnosed and redescribed, and its recent placement in the subfamily Deraeocorinae is confirmed. The new species *A. mindanao* and *A. palawanensis* from the Philippine Islands, and *A. pallidus* from Sabah and Sarawak are diagnosed and described. Lectotypes are designated for the Distant species *A. fractus* and *A. maurus* based on syntypic material preserved in the Natural History Museum, London. Illustrations are provided for the male genitalic structures of all species, and scanning electron micrographs are presented for the scent gland ostiole and pretarsus of *A. maurus*. A key is provided which uses external features and characters of the male genitalia to distinguish the five known species.

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Key words. – Heteroptera; Miridae; Deraeocorinae; *Angerianus*; review; new species; Oriental region.

Angerianus was described by Distant (1904) to accommodate two new species, *fractus* and *maurus*, collected at Myitta in the Tenasserim Valley, Burma. The genus was placed in the tribe Dicyphini by Carvalho (1952), but Cassis (1984), in a revision of this group, moved *Angerianus* into the Deraeocorinae. Stonedahl and Cassis (1991) present character information suggesting that *Angerianus* is most closely related to the Old World genus *Fingulus* Distant. In conjunction with that study, three new species of *Angerianus* were discovered in the entomological collections of the Bernice P. Bishop Museum, Honolulu. Descriptions of these species are provided here along with redescriptions of *fractus* and *maurus*, and a key to distinguish the five known species.

All measurements are given in millimeters. Body length is measured from the apex of the tylus to the deepest point of the cuneal incisure. Abbreviations used in the locality data to denote specimen depositories correspond to the institutions listed in the acknowledgments.

SYSTEMATIC ACCOUNT

Angerianus Distant

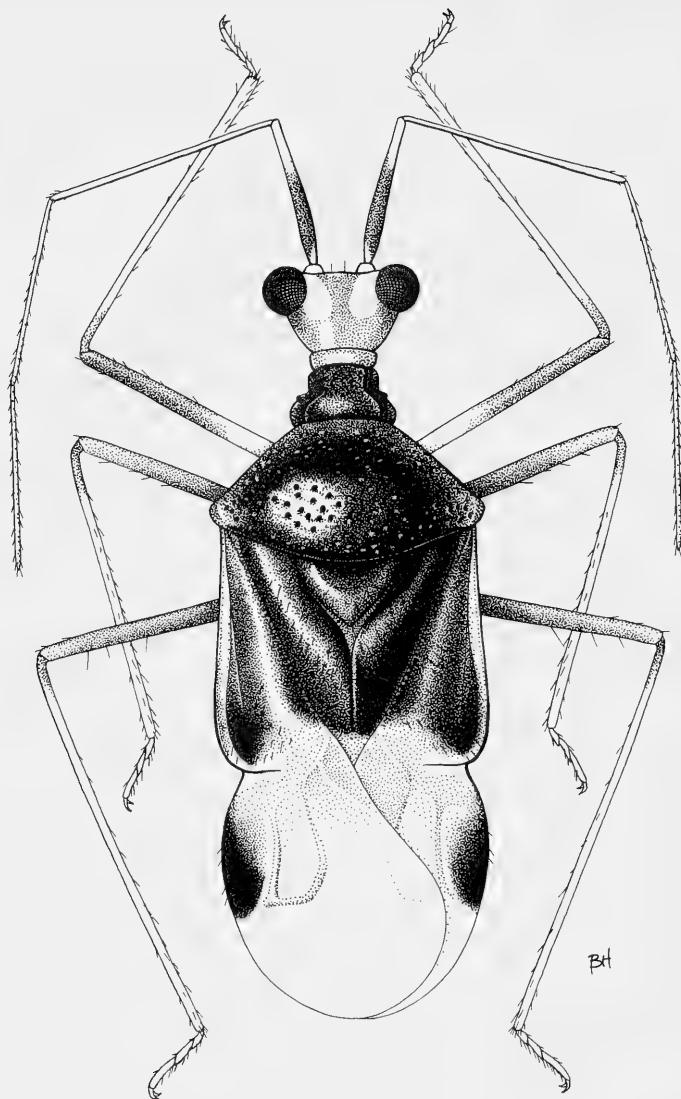
Angerianus Distant, 1904: 437-438. – Type species: *Angerianus fractus* Distant.

Angerianus: Reuter 1910: 161 (cat.); Carvalho 1952: 72 (classif., cat.), 1955: 60 (key), 1957: 182 (cat.); Cassis 1984: 166 (diag., subfam. placement).

Diagnosis. – Recognized by the head not produced anteriorly of eyes, with vertical frons and tylus; well developed cephalic neck; long first antennal segment; broad pronotal collar; lateral margins of pronotum constricted at level of anterior and posterior borders of calli; strongly deflexed hemelytra with broad, deep cuneal incisure; long, tapered femora (fig. 1); strongly protruding scent gland ostiole (figs. 2, 3); and structure of the male genitalia, especially the vesica without lobal sclerites, and no serrate plates bordering secondary gonopore.

Redescription of male. – Macropterous, length 2.19-2.77; pale brownish yellow to dark brown general coloration; dorsal surface shiny, smooth; collar and disc of pronotum finely to coarsely punctate; dorsal vestiture with moderate to dense distribution of long, pale setae, or sometimes nearly glabrous with shorter, scattered setae. Head: Vertical anteriorly, not produced distad of eyes, with weakly produced tylus; broader than long in dorsal view with vertex nearly twice as broad as dorsal width of eye; tapered posterior of eyes into distinct necklike region, with eyes well removed from anterior margin of pronotum; neck anteriorly with

Fig. 1. *Angerianus maurus*, dorsal habitus female.



transverse dorsal depression; eyes occupying nearly entire height of head in lateral view. Antennae: Long, thin, inserted well dorsad of median level of eyes; length of segment I equal to or greater than width of head across eyes; segments II-IV with moderately long, suberect, pale setae. Labium: Reaching to meso- or metacoxae; segments I-III similar in length, segment IV slightly longer. Pronotum: Strongly narrowed anteriorly and noticeably constricted at level of posterior margin of calli and at juncture of collar and calli; collar much broader than diameter of antennal segment I, flattened or weakly convex dorsally; calli confluent medially,

reaching lateral margins of pronotum, surface smooth or faintly rugulose, sometimes with long, pale setae; posterior margin of disc broadly convex, concealing most of mesoscutum and sometimes anterior margin of scutellum; scutellum elevated above resting hemelytra; metathoracic scent efferent system with strongly protruding ostiole, evaporative area not or only slightly extending dorsad of upper margin of ostiole. Hemelytra: Strongly deflexed at cuneal fracture; lateral margins nearly straight anteriorly, curving inward distally to broad, deep cuneal incisure; costal vein and claval suture marked by row of coarse punctures; cuneus

relatively long, with curved outer margin; membrane reaching well beyond apex of abdomen, with large primary cell and obsolete secondary cell. Legs: Femora elongate, tapered, broadest basally; tibiae and tarsi cylindrical, with pale, suberect setae; pretarsal claws strongly curved with prominent basal tooth (fig. 5). Genitalia: Genital capsule: Small, narrow, ventral region between paramere sockets slightly produced posteriorly; aperture large, posteriorly directed; paramere sockets asymmetrical with left socket slightly larger and ventrad of right socket. Left paramere: L-shaped with weakly to moderately produced sensory lobe; shaft long, tapered distally to blunt, sometimes truncate apex. Right paramere: Small, ovate to lanceolate, sometimes strongly narrowed distally; apex blunt. Phallosome: Short, conical, narrowly opened dorsodistally. Vesica: Composed of multilobed membranous sac surrounding distal region of ductus seminis, and simple, unmodified secondary gonopore opening into depressed area between membranous lobes. Lobes of vesica sometimes with patches of blunt tubercles, but lacking lobal sclerites. Basal region of vesica not surrounded by sclerotized skirt, and without serrate plates bordering secondary gonopore.

Female. – Macropterous, length 2.22–2.73; similar to male in general structure and coloration except as noted in species descriptions. Genitalia not examined.

Distribution. – Tropical Asia from Nepal east to Taiwan, the Philippine Islands and Sabah, and south to Java.

Discussion. – Distant (1904) placed *Angerianus* in the Division Cylaparia (Cylapinae), but Reuter (1910), uncertain of its relationships, treated this genus as incertae sedis in his classification of the Miridae. Apparently unaware of its distinct deraeocorine pretarsus and male genitalia, Carvalho (1952) moved *Angerianus* into the tribe Dicyphini (Phylinae). The correct subfamilial placement of *Angerianus* was established by Cassis (1984), who noted that members of this genus have a typical deraeocorine pretarsus, with cleft claw bases and setiform parempodia. Cassis also observed that the structure of the mesepimeric spiracle and the metaepisternal scent efferent system were like those of the Deraeocorinae and not the Dicyphini. The observations of Cassis are confirmed in the present study, and it is further noted that the male genitalic structures of *Angerianus* support its placement in the Deraeocorinae, particularly the shape of the left paramere and the depressed, unmodified secondary gonopore of the vesica.

The relationship of *Angerianus* to other deraeocorine genera is not well established. Cassis

(1984) tentatively regarded *Angerianus* as most closely related to the Hyaliodini, based primarily on the strongly protruding, tubelike auricle of the metaepisternal scent efferent system. Commenting on the similarities between *Angerianus* and *Stethoconus* Flor, Cassis questioned the placement of the later genus in the Clivinimini by Kerzhner (1967). *Stethoconus* has since been moved into the Hyaliodini by Henry et al. (1986).

In a recent revision of the Old World deraeocorine genus *Fingulus* Distant, Stonedahl and Cassis (1991, in press) suggested a possible sister group relationship between this genus and *Angerianus* based on characters of the external morphology and male genitalia. Further, these authors noted that *Fingulus* and *Stethoconus*, while superficially similar, have very different male genitalia and head morphology, indicating that they are not as closely related as originally suggested by Cassis (1984). Based on these preliminary findings, I consider *Angerianus* to be most closely related to *Fingulus*, but can say little about the relationships of these genera to other Deraeocorinae, except to suggest a possible link with the Hyaliodini.

Key to species of *Angerianus*

1. Collar and disc of pronotum with numerous coarse punctures and long, pale setae 2
- Collar and disc of pronotum with scattered fine punctures and short setae, or impunctate and appearing glabrous 4
2. Antennal segment I narrowly pale basally, brown or black distally; length of segment noticeably greater than width of head across eyes; male genitalia as in figures 12–14 *mindanao* sp. n.
- Antennal segment I darkened basally and pale distally; length of segment about equal to width of head across eyes 3
3. Fore femora mostly pale, sometimes lightly infuscated medially or rarely more extensively darkened distally; scutellum usually with large, pale spot distomedially; length of antennal segment II 1.24–1.44; male genitalia as in figures 6–8 *fractus* Distant
- Fore femora mostly fuscous, basal fourth pale; scutellum uniformly darkened, without pale spot medially; length of antennal segment II 1.02–1.17; male genitalia as in figures 9–11 *maurus* Distant
4. Pale brownish yellow general coloration; head uniformly pale; length of labium about equal to posterior width of pronotum; male genitalia as in figures 18–20 *pallidus* sp. n.
- Dark brown general coloration; head infuscated posteriad of eyes, and with dark stripe reaching from dorsal margin of antennal fos-

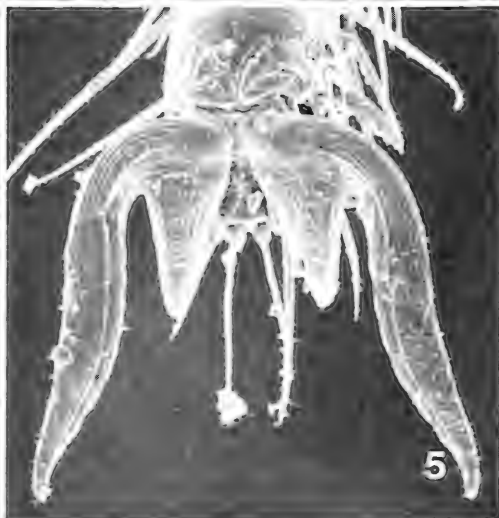
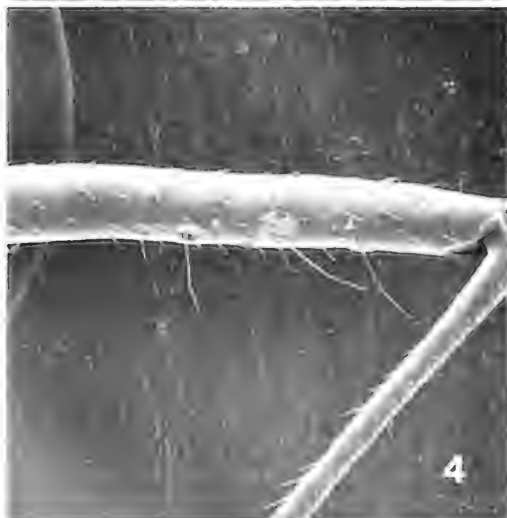
sae to posterior margin of head; length of labium much greater than posterior width of pronotum; male genitalia as in figures 15-17
..... *palawanensis* sp. n.

***Angerianus fractus* Distant**
(figs. 6-8)

Angerianus fractus Distant, 1904: 438, fig. 283. Lectotype ♀ (new designation): Label 1, 'Type, H.T.' [red-bordered disc]; 2, '*Angerianus fractus* Dist.' [handwritten]; 3, 'Tenass Vall, Myitta, (Doherty).'; 4, 'Distant Coll., 1911-383'; 5 (red label added here), 'Lectotype, *Angerianus fractus* Distant, det. by G. M. Stonedahl, 1991.' (NHML) [examined].
Angerianus fractus; Carvalho 1957: 182 (cat.).

Diagnosis. – Recognized by the coarsely punctate collar and disc of the pronotum; bicolored first antennal segment, with distal region pale; dark scutellum, usually with large, pale spot distomedially; and by the structure of the male genitalia (figs. 6-8). This species is further distinguished from *maurus* by the longer second antennal segment and mostly pale fore femora.

Description of male. – Length 2.37-2.52; yellowish brown to dark brown general coloration. Head: Width across eyes 0.66-0.70, vertex 0.30-0.33; mostly pale anteriorly and dorsally; gula and neck-like region posteriad of eyes brown or dark brown; lorum, buccula and gena usually lightly to heavily



Figs. 2-5. Scanning electron micrographs of *Angerianus maurus*. – 2, Lateral view of thorax; 3, Ostiole and evaporative area of metathoracic scent efferent system; 4, Metafemur showing trichobothria; 5, Pretarsus.

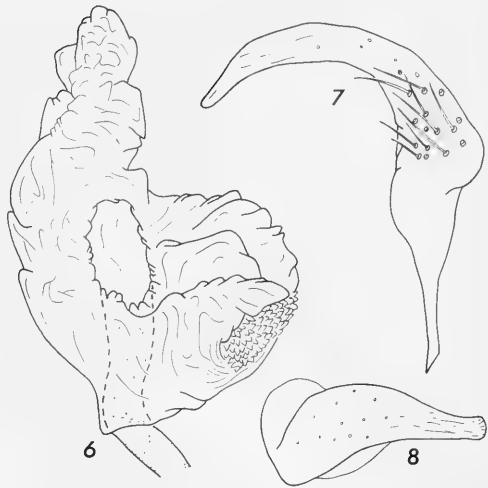
tinged with fuscous; vertex with V-shaped mark running from antennal fossae to depressed line marking anterior margin of neck. Antennae: I, length 0.62-0.70, basal half to two-thirds brown or dark brown, or in paler specimens sometimes only narrowly darkened basally, distal region pale yellow or dirty white; II, length 1.25-1.44, pale brownish yellow; III & IV, brown. Labium: Length 1.17-1.22; reaching between mesocoxae; segments I-III reddish brown, segment IV brownish yellow. Pronotum: Posterior width 1.16-1.25; collar and disc coarsely punctate; yellowish brown to dark brown, lighter specimens usually considerable darker laterally; scutellum brown or dark brown, usually with large pale spot distomedially; scent gland ostiole grayish white, much paler than surrounding pleura. Hemelytra: Dark yellowish brown to mostly dark brown – lighter specimens usually with apex of clavus, distal region of embolium and cuneus darker brown or brownish red; darker specimens with apical angle of corium and base of cuneus noticeably paler; membrane lightly to moderately tinged with fuscous basally, sometimes to level of apex of cuneus, veins brown or dark brown. Legs: Grayish yellow or brownish yellow; femora of lighter specimens usually with middle third infuscated, darker specimens usually with femora more extensively darkened distally and with base of tibiae narrowly darkened. Genitalia: Left paramere and vesica as in figures 6-8.

Female. – Length 2.34-2.50; width across eyes 0.65-0.67, vertex 0.31-0.32; length of antennal segment I 0.62-0.67, segment II 1.24-1.29; length of labium 1.08-1.20; posterior width of pronotum 1.17-1.27. Similar to male in structure and color, except second antennal segment usually much shorter, and pronotum broadly pale behind calli and with distinct pale stripe medially on disc.

Distribution. – Burma, Laos, Nepal, Thailand and Vietnam.

Discussion. – This species is quite variable in general coloration, ranging from yellowish brown with limited darker brown markings to mostly dark brown (see description of male). Females are less variable than males in coloration, and are always easily distinguished from other species of *Angerianus* by the pale, median stripe on the pronotal disc.

The original description of *A. fractus* gives Myitta, Tenasserim as the type locality. Although there is no indication of the number and sex of the specimens that Distant examined, it is clear from the habitus illustration and text that he was describing the female of this species. Two specimens of *A. fractus* from the type locality are deposited in the Natural History Museum in London. The female is here designated the lectotype, but it is



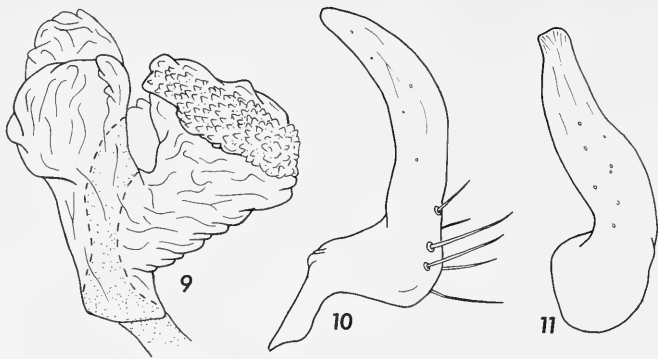
Figs. 6-8. Male genitalia of *Angerianus fractus*. – 6, Vesica; 7, Left paramere, dorsal view; 8, Left paramere, posterolateral view.

questionable whether the male specimen then becomes a paralectotype, as there is no evidence to suggest that Distant ever looked at specimens of this sex.

The head and prothorax of the lectotype have at some point been dislodged from the body and are now glued to the card point. All of the legs are missing, and only the first segment and base of the second segment of the right antenna remain.

Specimens examined. – Burma: Tenasserim: 1 ♂, same data as lectotype (NHML); 1 ♀ Dawna Hills, 2000-3000 ft, March 2-3, 1908 (NHML, Distant Coll.). – Laos: Vientiane Prov.: 1 ♀, Ban Van Eue, SE of Phou Kow Kuei, 800 m, April 14, 1965, J.L. Gressitt (BISH); 1 ♂, Ban Van Eue, Dec. 31, 1965, native collector (BISH). – Nepal: 1 ♂, Chitwan, Sauraha, Dec. 27, 1981-Jan. 9, 1982, *Shorea robusta* ('Sal') forest, on low vegetation, L. Jessop (NHML); 2 ♂, 1 ♀, Mugling, 900-1500 ft, Jan. 14-Feb. 5, 1982, mixed scrub on south facing slopes, L. Jessop (AMNH, NHML). – Thailand: Chiang Mai Prov.: 1 ♂, 1 ♀, Banna, 108 m, May 5-10, 1958, T.C. Maa (BISH); 1 ♂, 1 ♀, Chiangdao, 450 m, April 5-11, 1958, T.C. Maa (BISH); 1 ♀ Doi Sutthop, Nov. 14, 1957, J.L. Gressitt (BISH); 1 ♂, 4 ♀, Fang, April 12-19, 1958, T.C. Maa (BISH); 1 ♂, Fang Hort. Exp. Stn., 550-600 m, Oct. 20, 1981 (UZMC). Trang Prov.: 1 ♂, Khaophapha, Khaochang, 200-400 m, Jan. 13, 1964, G.A. Samuelson (BISH). – Vietnam: 1 ♂, 1 ♀, Ban Me Thout, 500 m, Dec. 20-24, 1960, C.M. Yoshimoto (BISH); 1 ♀, 6 km s of Dalat, 1400-1500 m, June 9-July 7, 1961, N.R. Spencer (BISH).

Figs. 9-11. Male genitalia of *Angerianus maurus*. – 9, Vesica; 10, Left paramere, dorsal view; 11, Left paramere, posterolateral view.



***Angerianus maurus* Distant**
(figs. 1-5, 9-11)

Angerianus maurus Distant, 1904: 438. Lectotype ♂ (new designation): label 1, 'Tenass Vall, Myitta, (Doherty)'; 2, 'Distant Coll., 1911-383'; 3 (red label added here), 'Lectotype, *Angerianus maurus* Distant, det. by G. M. Stonedahl, 1991.' (NHML) [examined].

Angerianus maurus; Carvalho, 1957: 182 (cat.).

Diagnosis. – Similar to *A. fractus*, but distinguished by the darker legs, uniformly darkened scutellum and shorter second antennal segment. Males are further distinguished by the narrower vertex, longer labium, and structure of the genitalia (figs. 9-11).

Description of male. – Length 2.19-2.37; brown to dark brown general coloration. Head: Width across eyes 0.66-0.70, vertex 0.24-0.26; brown or dark brown; frons, tylus, jugum, lorum and gena usually paler brownish yellow; vertex with broad, pale mark bordering inner margin of each eye. Antennae: I, length 0.63-0.67, basal two-thirds dark brown, distal region pale yellow or dirty white; II, length 1.12-1.17, pale brownish yellow; III & IV, brown. Labium: Length 1.06-1.10; reaching between meso- or metacoxae; segments I-III dark reddish brown, segment IV brownish yellow. Pronotum: Posterior width 1.09-1.13; collar and disc coarsely punctate; uniformly brown or dark brown; scent gland ostiole yellowish white, much paler than surrounding pleura, evaporative area sometimes lightly tinged with fuscous. Hemelytra: Brown or dark brown; anterior half of embolium, apex of corium, and basal margin of cuneus noticeably paler; membrane lightly tinged with fuscous basally, sometimes to level of apex of cuneus, veins brown or dark brown. Legs: Brownish yellow, with distal two-thirds of femora and base of tibiae usually dark brown. Genitalia: Figures 9-11.

Female. – Length 2.22-2.40; width across eyes 0.62-0.66, vertex 0.26-0.28; length of antennal seg-

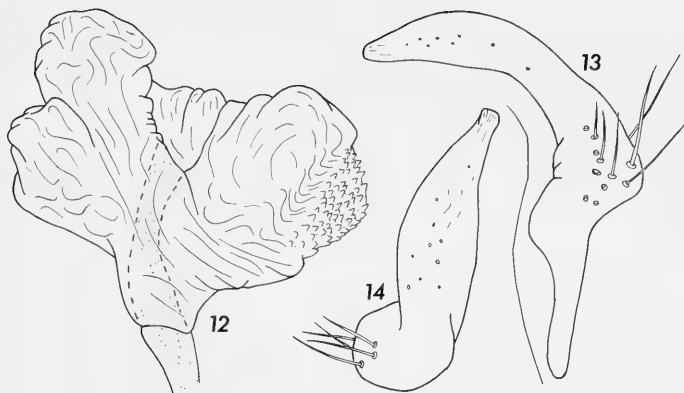
ment I 0.64-0.69, segment II 1.02-1.11; length of labium 1.06-1.13; posterior width of pronotum 1.13-1.18.

Distribution. – Widely distributed in tropical Asia from Nepal, east to Taiwan and Sabah, and south to Java.

Discussion. – Like *A. fractus*, this species was described from a unknown number of specimens collected at Myitta in the Tenasserim Valley, Burma. Four specimens apparently belonging to the original syntype series are deposited in the Natural History Museum in London. One of these is here designated the lectotype and the others become paralectotypes.

Paralectotypes. – 1 ♂ (head and pronotum missing), 1 ♀, same data as lectotype; 1 ♀, same data as lectotype except with two additional labels below specimen as follows: Label 1, 'Type, H.T.' [red-bordered disc]; 2, '*maurus* Dist.' [handwritten]. A yellow label with the following data has been added to each of these specimens: 'Paralectotype, *Angerianus maurus* Distant, det. by G. M. Stonedahl, 1991.' All paralectotypes are deposited in the Natural History Museum, London.

Specimens examined. – Cambodia: 1 ♀, Siem Reap (Angkor), Dec. 6, 1957, J. Szent-Ivany (BISH). – Indonesia: Java: 1 ♀, S Coast, Tankubanpraku, Sept. 27, 1960, forest remnant, J.L. Gressitt (BISH). – West Malaysia: Pahang: 1 ♀, Dec. 22-26, 1958, T.C. Maa (BISH). Penang: 1 ♀, Oct. 1913, G.E. Bryant (NHML); 1 ♀, Island of Penang, Baker (USNM). – Sabah: 2 ♂, Liawan, Jan. 14-19, 1959, sweeping, T.C. Maa (BISH); 1 ♀, Samawang, nr. Sandakan, July 14, 1927 (NHML). – Sarawak: 1 ♂, Merirai Valley, nr. Kapit, 30-300 m, July 1-6, 1958, T.C. Maa (BISH). – Nepal: 2 ♀, Chitwan, Sauraha, Dec. 27, 1981-Jan. 9, 1982, *Shorea robusta* ('Sal') forest, on low vegetation, L. Jessop (NHML). – Taiwan: 1 ♀, Menzendo, '1-6-33,' native pineapple field, K. Sakimura (BISH); 1 ♂, Pishan, Nov. 14, 1957, T.C. Maa (BISH). – Thailand: 1 ♂, 3 ♀, Pakchong, 100 m, NE of Bangkok, Dec. 2-3, 1957, J.L. Gressitt (BISH). Chiang Mai Prov.: 1 ♀, Chiangdao, April 5-11, 1958, T.C. Maa (BISH); 1 ♂, 1 ♀, Fang, April 12-19, 1958,



Figs. 12-14. Male genitalia of *Angerianus mindanao*. – 12, Vesica; 13, Left paramere, dorsal view; 14, Left paramere, postero-lateral view.

T.C. Maa (BISH). – Vietnam: 1 ♂, Ap Hung-Lam, 21 km NW of Dilinh, 1100 m, Sept. 29-Oct. 5, 1960, C.M. Yoshimoto (BISH); 7 ♂, 2 ♀, Ban Me Thout; 500 m, Dec. 20-24, 1960, C.M. Yoshimoto (BISH); 1 ♀, Karyu Danar, 200 m, Feb. 13-28, 1961, N.R. Spencer (BISH); 1 ♂, 1 ♀, M'Drak, E of Ban Me Thout, 400-600 m, Dec. 8-19, 1960, C. M. Yoshimoto (BISH).

Angerianus mindanao sp. n.
(figs. 12-14)

Type material – Holotype ♂: Philippine Islands: Mindanao: Davao del Sur: Galog R., Mt. Apo, 6000 ft, Sept. 26, C.S. Clagg (AMNH). – Paratypes: Philippine Islands: Mindanao: Davao del Sur: 1 ♀ (Sept. 5) and 4 ♀ (Sept. 26), same data as holotype (AMNH); 1 ♀, Mt. Apo, Batraeyon, 8000 ft, Sept. 14, C.S. Clagg (AMNH); 1 ♂, Mt. Apo, Mainit R., 6000 ft, Sept. 24, C.S. Clagg (NHML).

Additional Specimens. – Philippine Islands: Mindanao: Bukidnon: 2 ♀, Mt. Katanglad, 1250 m, Oct. 26, 1959, L.W. Quate (BISH); 1 ♂ (badly damaged, with head, hemelytra and all but one leg missing), Mt. Katanglad, 1250 m, Dec. 4-9, 1959, L.W. Quate (BISH); 1 ♀, Mt. View Colleges, 15 km NW of Valencia, April 22-23, 1968, D.E. Hardy (BISH).

Diagnosis. – Recognized by the coarsely punctate pronotal collar and disc, dark brown first antennal segment with basal sixth to one-third pale, and by the structure of the male genitalia (figs. 12-14). This species is further distinguished from *fractus* and *marus* by the longer first antennal segment and darker scent gland ostiole.

Description of male. – Length 2.40-2.56; brownish yellow to dark brown general coloration. Head: Width across eyes 0.66-0.69, vertex 0.29-0.32; brownish yellow, usually slightly darker ventrally, especially posteriad of eyes; head of darker specimens brown or dark brown, with frons and vertex paler brownish yellow. Antennae: I, length 0.80-0.84, fuscous, with basal sixth to one-third pale; II, length 1.15-1.19, yellowish brown; III & IV,

brown. Labium: Length 1.25-1.39; reaching between meso- or metacoxae; segments I-III reddish brown, segment IV yellowish brown. Pronotum: Posterior width 1.17-1.24; collar and disc coarsely punctate; uniformly yellowish brown, sometimes with collar and calli slightly darker; darkest specimens with collar, calli and margins of disc dark brown and medial region of disc lighter brown; scutellum brown or yellowish brownish; scent gland ostiole brown or yellowish brown, not or only slightly paler than surrounding pleura. Hemelytra: Brownish yellow to mostly dark brown; membrane sometimes tinged with fuscous basally, veins brown or brownish yellow. Legs: Uniformly brownish yellow, or in darker specimens, with distal half to two-thirds of femora, and sometimes base of tibiae darker brown. Genitalia: Left paramere and vesica as in figures 12-14.

Female. – Length 2.48-2.60; width across eyes 0.64-0.66, vertex 0.31-0.33; length of antennal segment I 0.77-0.84, segment II 0.99-1.06; length of labium 1.24-1.42; posterior width of pronotum 1.12-1.20.

Etymology. – Named for the island of Mindanao.

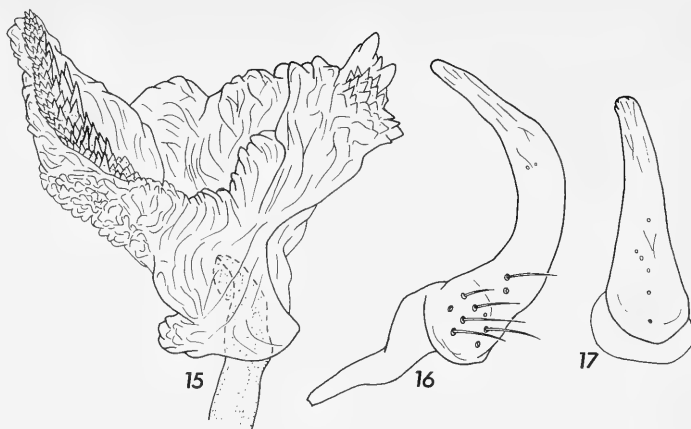
Distribution. – Mindanao, Philippine Islands.

Discussion. – This species is quite variable in general coloration, the dorsum ranging from uniformly pale brownish yellow (type and paratypes from Mt. Apo) to mostly brown or dark brown (Bukidnon specimens). The ventral parts of all the examined specimens are extensively darkened. An examination of external morphological features and the male genitalia of specimens from these two areas confirmed that they belong to a single species.

Angerianus palawanensis sp. n.
(figs. 15-17)

Type material. – Holotype ♂: Philippine Islands: Pa-

Figs. 15-17. Male genitalia of *Angerianus palawanensis*. – 15, Vesica; 16, Left paramere, dorsal view; 17, Left paramere, postero-lateral view.



lawan: Mantalingajan, Pinigisan, 600m, Sept. 6, 1961 (UZMC, Noona Dan Exp.).

Diagnosis. – Recognized by the dark brown general coloration, with legs and antennae mostly pale; head with broad, longitudinal stripe between eyes; pronotum appearing glabrous, with scattered, fine punctures on collar and disc; length of labium much greater than posterior width of pronotum, and male genitalia as in figures 15-17.

Description of male holotype. – Length 2.30; dark brown general coloration. Head: Width across eyes 0.66, vertex 0.31; pale brownish yellow, except dark brown posteriad of eyes ventrally and laterally, and with fuscous stripe between eyes extending to anterior margin of pronotum. Antennae: I, length 0.77, basal half dark yellowish brown, distal half slightly paler; II, length 1.59, pale brownish yellow; III & IV, brown. Labium: Length 1.31; reaching to posterior margin of metacoxae; segments I & II dark brown, III & IV pale brownish yellow. Pronotum: Posterior width 1.06; collar and disc with scattered fine punctures, appearing glabrous; uniformly dark brown, except somewhat paler laterally dorsad of coxal cleft; scutellum dark brown, less strongly elevated above level of hemelytra; scent gland ostiole dark brown, similar in coloration to surrounding pleura. Hemelytra: Clavus and corium dark brown, becoming slightly paler distally; cuneus brown basally, outer margin and apex broadly pale, almost clear; membrane lightly tinged with fuscous basally, veins brown, paler distally. Legs: Uniformly pale yellow. Genitalia: Figures 15-17.

Female. – Unknown.

Etymology. – Named for its occurrence on the island of Palawan.

Distribution. – Palawan, Philippine Islands.

Angerianus pallidus sp. n.
(figs. 18-20)

Type material. – Holotype ♂: Malaysia: Sarawak: Nanga Pelagus, nr. Kapit, 180-585 m, Aug. 7-14, 1958, T.C. Maa (BISH). – Paratype: Malaysia: Sabah: 1 ♂, Ranau, Sept. 30-Oct. 5, 1958, T.C. Maa (BISH).

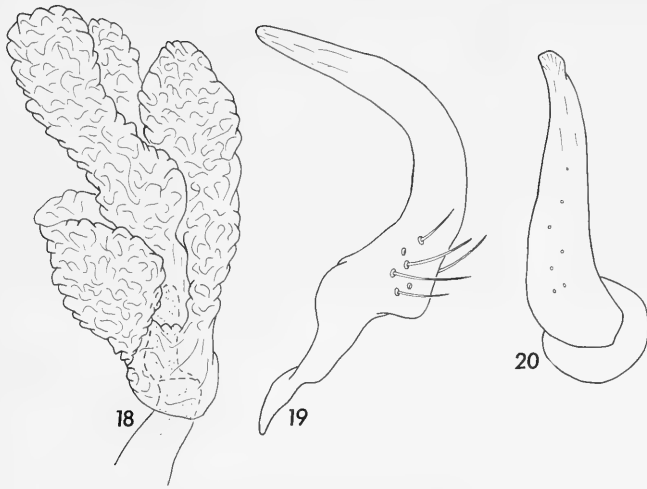
Diagnosis. – Similar to *mindanao* in size and general coloration, but distinguished by the broader head and vertex, weakly punctate pronotal disc, and structure of the male genitalia (figs. 18-20). The pale general coloration and faint punctures on the pronotal disc will distinguish *pallidus* from *fractus*, *maurus* and *palawanensis*.

Description of male. – Length 2.55-2.77; pale brownish yellow general coloration. Head: Width across eyes 0.73-0.77, vertex 0.36-0.39; uniformly brownish yellow. Antennae: I, length 0.88, pale brownish yellow; II-IV, missing. Labium: Length 1.39; reaching between mesocoxae; uniformly pale brownish yellow. Pronotum: Posterior width 1.38; brownish yellow; collar and disc with very faint, shallow punctures and short, pale setae; scutellum brown or pale grayish yellow, moderately elevated above level of resting hemelytra; scent gland ostiole dirty yellow, only slightly paler than surrounding pleura. Hemelytra: Clavus brown or grayish yellow; corium and cuneus clear pale yellow – corium of holotype lightly tinged with fuscous basally, especially bordering claval suture; membrane clear, with slight yellow coloration bordering veins. Legs: Uniformly pale brownish yellow. Genitalia: Left paramere and vesica as in figures 18-20.

Female. – Unknown.

Etymology. – From the Latin, *pallidus* (pale), referring to the pale general coloration.

Distribution. – Sabah and Sarawak, Malaysia.



Figs. 18-20. Male genitalia of *Angerianus pallidus*. – 18, Vesica; 19, Left paramere, dorsal view; 20, Left paramere, posterolateral view.

Discussion. – The paratype of this species is uniformly pale dorsally, while the holotype has the scutellum and clavus darker than the rest of the dorsum. All other features of the two specimens including the male genitalia are indistinguishable, although it is noted that the holotype is slightly larger than the paratype.

ACKNOWLEDGMENTS

I thank the following individuals and their respective institutions for providing specimens for study: Randall T. Schuh, American Museum of Natural History, New York (AMNH); Gordon M. Nishida, Bernice P. Bishop Museum, Honolulu (BISH); William R. Dolling, Natural History Museum, London (NHML); Richard C. Froeschner and Thomas J. Henry, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Nils Møller Andersen, Universitetets Zoologiske Museum, Copenhagen (UZMC). Bonnie B. Hall, Scientific Illustrator, Systematic Entomology Laboratory, Department of Entomology, Oregon State University prepared the dorsal habitus illustration of *Angerianus maurus*, with funds made available by the Oregon State University Foundation (Systematic Entomology Laboratory Fund). Assistance with preparation of the scanning electron micrographs was received from John Spratt and Susan Barnes, SEM Unit, NHML.

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Received: 25 March 1991

Accepted: 2 July 1991

Continued from p. 200

area. The ecological section deals with zonation of dung and carrion beetles and Lepidoptera, and includes specialized studies on several groups of Coleoptera, Hymenoptera, Diptera, Lepidoptera and aquatic Acari. A list of the publications related to the expedition concludes the volume.

My opinion on this publication cannot be objective. Working myself on the Odonata of Sulawesi, I am interested in every paper on this island. Of course I love to see the forest profiles of the places

I have worked myself. The extensive contributions on the aquatic fauna make this publication even more attractive to me. On the other hand, this book presents so many new and interesting data, that I am convinced that it deserves a broader readership than the expedition members alone. I can warmly recommend it to anybody interested in tropical entomology. The book is good value for money, although the quality of typesetting and printing is below one would expect for the final presentation of such an important enterprise.

[J. van Tol]

CORRIGENDA

Gielis, C., 1991. *Pterophorus* Schäffer in the Ethiopian region (Lepidoptera: Pterophoridae: Pterophorinae): new species and checklist. – Tijdschrift voor Entomologie 134: 1-8, figs. 1-21.

The editors regret that the plates on pages 4 and 6, in the above mentioned paper, showing the female genitalia, were incorrectly composed, so that the figure numbers for figs. 10-20 were wrongly assigned.

The following key gives the correct figure numbers:

10	change into:	15
11	change into:	16
12	change into:	17
13	change into:	18
14	change into:	19
15	change into:	20
16	change into:	10
17	change into:	11
18	change into:	12
19	change into:	13
20	change into:	14
21	remains:	21

For convenience, we also include adapted captions for page 4 and 6 respectively:

page 4:

Figs. 15-20. – *Pterophorus* spp., female genitalia. – 15, *P. candidalis* (Walker), Côte d'Ivoire, slide CG 2182 (CG); 16, *P. candidalis* (Walker), Chad, slide CG 2186 (CG); 17, Idem, Tanzania, slide CG 4020 (ZMUC); 18, *P. dallastai* sp. n., paratype, slide CG 1851 (MRAC); 19, *P. massai* sp. n., holotype, 20, *P. uzungwe* sp. n., paratype, slide CG 4040 (ZMUC);

page 6:

Figs. 10-14. – 21. *Pterophorus* spp., female genitalia. 10, *P. alibidus* (Zeller), Tanzania, slide CG 4018 (ZMUC); 11, *P. rhyparias* (Meyrick), Zaire, slide Bigot (MRAC); 12, *P. ceraunia* (Bigot), Benin, slide CG 1881 (MNHN); 13, *P. lampira* (Bigot), Côte d'Ivoire, slide CG 2178 (CG); 14, *P. spissa* (Bigot), paratype, Zaire, slide Bigot (MRAC); 21, *P. cleronoma* Meyrick, paralectotype, slide Bigot (MNHN).

ECOLOGICAL CHARACTERIZATION OF CARABID SPECIES (COLEOPTERA, CARABIDAE) IN THE NETHERLANDS FROM THIRTY YEARS OF PITFALL SAMPLING

Turin, H., K. Alders, P. J. den Boer, S. van Essen, Th. Heijerman, W. Laane & E. Penterman, 1991. Ecological characterization of carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. – *Tijdschrift voor Entomologie* 134: 279-304, figs. 1-20, tabs. 1-10. [ISSN 0040-7496]. Published 18 December 1991.

An ecological characterization of 285 Dutch carabid species based on a large data set obtained by pitfall trapping in various habitats all over The Netherlands is presented. The data set contains ca. 1.5 million specimens, collected during thirty years in 1616 year-samples from 862 localities. Information about habitat, viz. type of vegetation, type of soil and humidity was recorded for each of the 862 sampling localities.

Two Way Indicator Species Analysis (TWINSpan) as well as Detrended Correspondence Analysis (DECORANA) were used to classify the species into habitat groups. Seven principal habitat groups could be recognized. Indices for ecological amplitude, preference for soil type and humidity, are formulated and estimated for each species. This resulted in a description of the habitat preferences of the Dutch carabid species in far greater detail than was possible before. The classification is compared with others from the literature. Correspondence: H. Turin, Esdoorndreef 29, 6871 LK Renkum. The Netherlands.

Key words. – Ecology, Carabidae, Twinspan, Decorana, pitfall

In 1945, Lindroth published the first volume of his major work 'Die Fennoskandischen Carabidae' (Lindroth 1945). In this work he described the ecological preferences of the Fennoscandian carabid species. Since pitfall trapping was not practiced until about 1950, Lindroth's ecological characterizations were based on his own hand-collections, supplemented by those of other collectors, on laboratory experiments and on data taken from literature. This resulted in detailed descriptions of the species' ecological preferences. In 1949, Lindroth classified the species into a number of ecological groups, recognizing xerophilous species, mesophilous species (including ubiquitous), hygrophilous species, arboreal species, forest species and synanthropic species (Lindroth 1949).

From about 1950 onwards, pitfall trapping became a commonly used technique in Europe. Thiele (1977) gave a summary of many ecological studies based on pitfall trapping carried out until ca. 1975. On basis of the results of these studies he characterized the carabid faunas of certain types of habitat, such as forests, sandy habitats and cultivated

land, by presenting lists of characteristic species of these habitat categories. However, his tables only show the most abundant species in that particular habitat group giving no information about the occurrences of these 'typical' species in other types of habitat.

Luff et al. (1989) were the first to classify habitats of ground beetles based on a large data set from nearly 250 sites in North-East England. The carabid samples were grouped, based on presence/absence data, using the Two Way Indicator Species Analysis (TWINSpan (Hill 1979a) and ordinated by Detrended Correspondence Analysis (DECORANA (Hill 1979b)). Ten primary groups of carabid habitats were recognized, viz.: coastal, upland (dry, wet), woodland, grassland (dry, wet), riverside (boulders, shingle, sand) and marsh. Eyre & Luff (1990a) made a preliminary classification of European grassland habitats using carabids. The carabid assemblages of 363 pitfalled grasslands throughout Britain, were described by Eyre & Luff (1990b).

The characterizations of Lindroth (1945, 1949)

are usually considered to be accurate, although they were obtained with a non-quantitative method. Furthermore, Lindroth's classification applies to the Fennoscandian situation, and species preferences may show geographical variation.

The major disadvantage of the analyses of Thiele (1977) is, that his compilations are based on data from the British Isles to Russia. Many of the species only occur in a limited part of this area.

The present study was carried out because there is a need for adequate ecological characterizations for the Dutch area with respect to future work, especially in the field of nature management and conservation. The material that is available from The Netherlands allows us to use quantitative methods to describe the ecological preferences of 285 species in our area in great detail. The ecological characterizations can serve as a basis for future descriptions and evaluations of carabid faunas of specific areas within The Netherlands.

MATERIAL AND METHODS

Material

When preparing the first edition of the Dutch carabid atlas (Turin, et al. 1977) it appeared that an

enormous amount of data from pitfall trapping was available. Pitfalls were used in The Netherlands already in the early 1950's by Van der Drift, soon followed by Den Boer in 1953.

In the past, several studies concerning the efficiency of pitfall sampling have been carried out. A summary of the results of these investigations up to 1975 was published by Thiele (1977), concluding that pitfall trapping is a suitable technique for investigating carabid populations in a quantitative way. Den Boer (1977, 1990) reviewed investigations carried out by pitfall sampling at the Biological Station Wijster. It appeared that so-called year-catches of most carabid species give reliable relative estimates of the mean densities of active adult specimens around the pitfalls (Baars 1979, Den Boer 1979). A year-catch is defined as the summation per species of all specimens caught in one series of pitfalls during one year (or at least during the main reproductive period of carabids). These estimates are relative, meaning that they can be used only to compare the relative abundances within a certain species over a series of samples and/or years, but not between species. This is because each species has characteristic 'catch-parameters', such as activity pattern, way of living and catchability (see Luff 1975, Den Boer 1986).

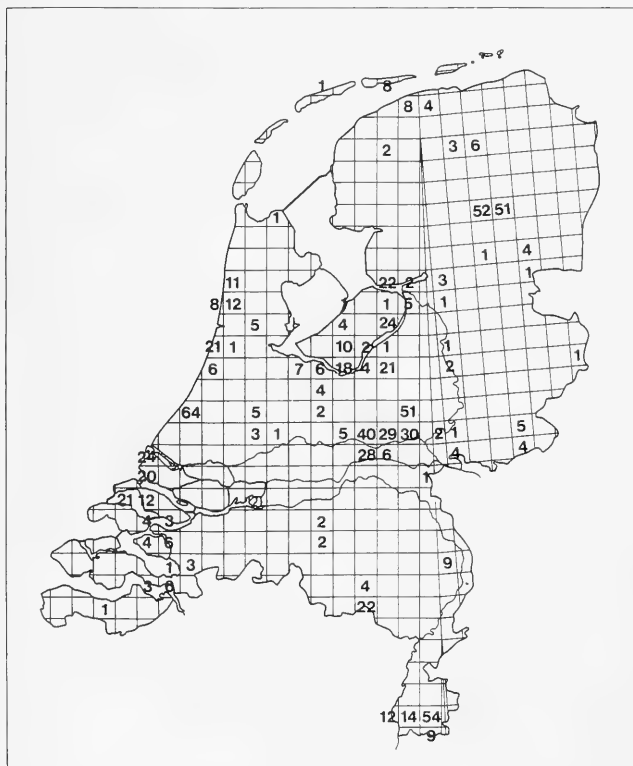


Fig 1. The number of sampled sites per 10 km square of the UTM-grid in the Netherlands.

The dataset for the present study consists of 1616 year-samples from 862 localities in The Netherlands (fig. 1), covering the period 1953-1983. A list of all year-samples included in the database is given by Turin & Penterman (1985).

The number of pitfalls used in a pitfall series and the sizes of the traps varied considerably between investigators. Therefore, the number of specimens in a year-sample were standardized by calculating the number of specimens per decimeter pitfall edge per year (SDY).

Before considering the catches, all sampling localities were uniformly described, using the 'eco-code' of the European Invertebrate Survey for The Netherlands (Van Tol 1979) in a slightly modified version (Penterman & Turin 1985). In this code information about type of vegetation, soil type, soil humidity, size of the locality and type of management is recorded. This information allowed us to recognize 33 habitats (table 1, p. 292), according to which the 1616 year-samples were coded.

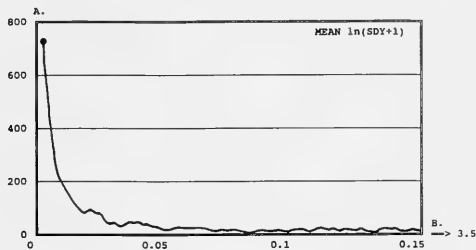


Fig. 2. The frequency distribution of the species mean $\ln(\text{SDY}+1)$ -values over each of the 33 habitats, taken from the data matrix. A: the Y-axis shows the number of relative abundances (see text) in the data matrix. B: the mean $\ln(\text{SDY}+1)$ -values; only a very small part of the X-axis is shown. This means that the values are very low all over the data matrix. These figures proved to be unwor-
kable for TWINSpan classification.

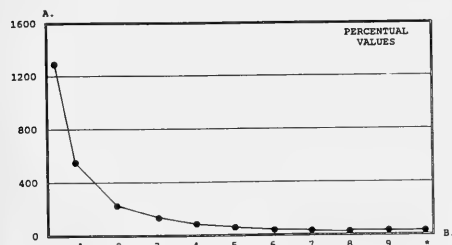


Fig. 3. The distribution of the pertage values after rescaling the mean abundances per species, with the maximum mean $\ln(\text{SDY}+1)$ put to 100% (relative occurrences). A: the Y-axis shows the number of relative occurrences. All figures from all 33 habitats are included except the first highest percentage value (* = 100%) of each species, which was used as a basic value for the rescaling. B: the percentage values, where: . = $\leq 5\%$, 1 = 5-15%, 2 = 15-25% etc., 9 = 85-95% and * = $\geq 95\%$; for further explanation see text and tables 2-9.

Classification of habitats and habitat preferences of species

Catches of a single carabid species from a large number of pitfall samples over many years, tend to form a log-normal distribution (Den Boer 1977). Therefore, the number of specimens per decimeter per year (SDY), was transformed to natural logarithms. For each of the 33 habitat categories (table 1) the mean value of $\ln(\text{SDY}+1)$ was calculated per species. Since all year-samples contribute to the mean $\ln(\text{SDY}+1)$ of a species, including those where the species was not recorded or in very low numbers only, the resulting values were very low for the majority of the species (fig. 2). Therefore, the values for the relative abundances were rescaled, by setting the highest value for a species at 100% and recalculating the SDY-values for the other habitats accordingly (fig. 3), in this way transforming the relative abundances into relative occurrences. This also made the catches of different species better comparable. We did not rescale the abundances of the species per habitat, in order to save the differences in significance between habitats as suitable sites for survival.

TWINSpan was applied to the relative occurrences of the species, to classify the habitats into habitat groups and to obtain a classification of the species according to their habitat preferences based on the rescaled mean $\ln(\text{SDY}+1)$ -values. TWINSpan was used using cut-levels 20, 40, 60 and 80% and was run several times using different pseudospecies' cut-levels. The results of these runs were all very similar when using the rescaled mean $\ln(\text{SDY}+1)$ -values. The results with different cut-levels based on the mean $\ln(\text{SDY}+1)$ values without rescaling, however, differed considerably among each other and were not further used. The resulting classification of habitats will be presented in the form of hierarchical tree diagrams and scattergrams. The full two-way table is presented, showing the group division of the species and containing the values indicating the relative occurrences as defined by the pseudospecies' cut levels. The information presented in this table allows us to easily evaluate the habitat specificity of a particular species.

Ecological amplitude

Two indices were defined and calculated that estimate the ecological amplitude of a species. The first measure (PRES) is based on the species presences over habitats, and is defined as:

$$\text{PRES}_j = \frac{n_j}{n}$$

where $PRES_j$ represents the ecological amplitude of the j -th species, n_j the number of habitats in which this species is present, and n the total number of habitats recognized (33). $PRES$ will range from 0 to 1.

For the second 'eurytopy' estimate (SIM) the index of Simpson (D) is used (Simpson 1949), which characterizes the distribution of the abundances over the habitats in the form of: $1-D$. This may thus be written as:

$$1 - \sum_{j=1}^n \left(\frac{a_j}{a_{tot}} \right)^2$$

where a_j is a measure of the relative abundance of a species in habitat group j and is equal to $\ln(SDY+1)_j$, while

$$a_{tot} = \sum_{j=1}^n \overline{\ln(SDY+1)}_j$$

The value of SIM may range from 0 to 1.

Soil type and humidity

When characterizing the sampling localities, three humidity classes were recognized, viz. 'dry', 'moist' and 'wet'. The humidity preference of a species was estimated at an ordinal scale from 1 (very xerophilous) to 5 (very hygrophilous). Species only caught in 'wet' localities score 5, species from 'wet' as well as from 'moist' localities score 4, species only from 'moist' localities score 3, species from 'moist' as well as from 'dry' localities score 2 and species only from 'dry' localities score 1.

Each sampling locality was also classified into one of seven soil types: limestone (li), loam (lo), loamy sand/sandy clay (ls), river clay (rc), sea clay (sc), peat moor (pm) and sand (s). A species is regarded to show a preference for a certain kind of soil when the $\ln(SDY+1)$, averaged over all localities with this specific soil type, is at least 2 times the sum of the mean $\ln(SDY+1)$ values of the localities from the other soil types taken together.

Nomenclature and taxonomy

The nomenclature follows Turin (1990), except for three *Calathus* species of the *melanocephalus* group, for which is referred to Aukema (1990). The material from pitfall trapping presented here under the name of *C. melanocephalus* in fact is a mixture of *C. melanocephalus* and *C. cinctus* (Aukema 1990). Only in the more recent sampling (ca. after 1980), *C. cinctus* was recognized as a separate

species. A similar problem exists where it concerns the species *Pterostichus nigrita* and *Asaphidion flavipes*. *Pterostichus rhaeticus* was not separated from *P. nigrita* (see: Koch 1984), and *Asaphidion curtum* as well as *A. stierlini* not from *A. flavipes* (see: Lohse 1983, Lompe 1989, Schweiger 1975). The full names of all species are given in the appendix.

RESULTS

Classification of habitats

Figs. 4-11 present the results from the TWINSpan classification of the relative occurrences over the 33 habitats from table 1. Seven main habitat groups could be recognized (fig. 4):

Group I. – Peat and heath vegetations, habitats 1-5. A further subdivision of this end-group is presented in fig. 5.

Group II. – Poor grassland and dune habitats, habitats 6-11 (subdivision see fig. 6).

Group III. – Cultivated land and open coniferous plantations, habitats 12-15 (subdivision see fig. 7).

Group IV. – Mature forests, habitats 16-20 (subdivision see fig. 8).

Group V. – Moist/wet forests (forests in water meadows; brook forests) and ruderal grass localities, including limestone grassland, habitats 21-25 (subdivision see fig. 9).

Group VI. – Moist habitats overgrown with weeds, polder-(colonization-) habitats, habitats 26-30 (subdivision see fig. 10).

Group VII. – Wet habitats/shores, habitat 31-33 (subdivision see fig. 11).

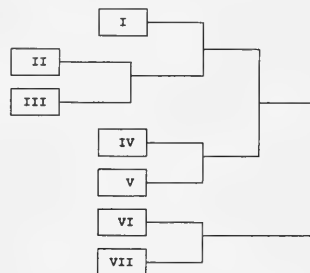
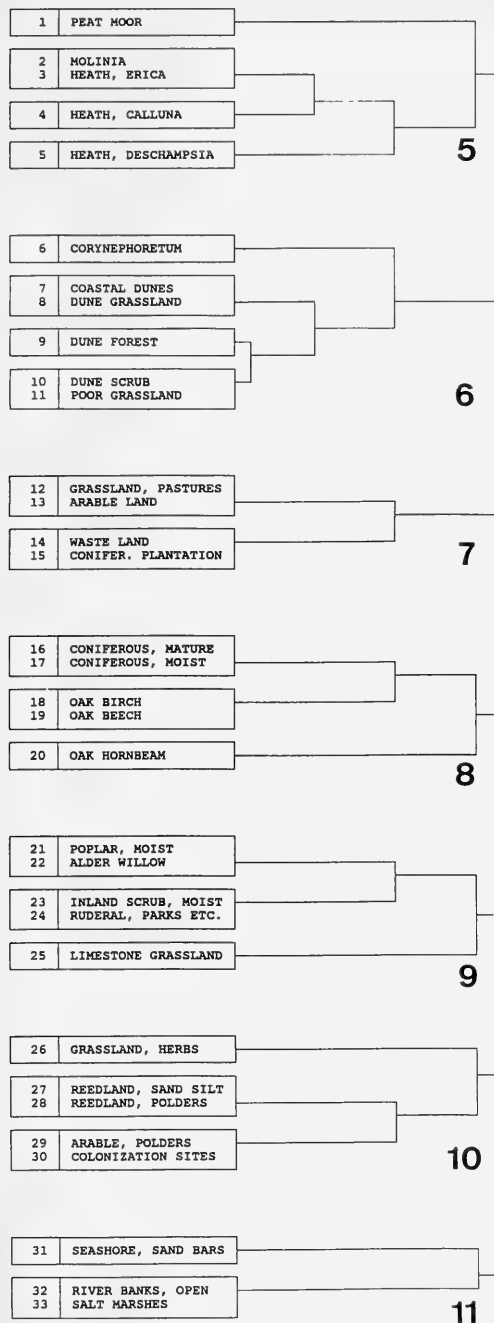


Fig. 4. Dendrogram of the main division into seven groups according to TWINSpan classification of the species' relative occurrences. I-VII = main habitat groups: I = Peat and heathland vegetations (habitat 1-5, see fig. 5), II = Poor grassland and dune habitats (habitat 6-11, see fig. 6), III = Cultivated land and open coniferous plantations (habitat 12-15, see fig. 7), IV = Mature forests (habitat 16-20, see fig. 8), V = Moist / wet forests and ruderal grass localities, including limestone grassland (habitat 21-25, see fig. 9), VI = Moist habitats, overgrown with weeds, polder-(colonization-) sites (habitat 26-30, see fig. 10), VII = Wet habitats/shores (habitat 31-33, see fig. 11).



Figs. 5-11. Subdivision of habitat groups I-VII (see fig. 4 and table 1). – 5, group I; 6, group II; 7, group III; 8, group IV; 9, group V; 10, group VI; 11, group VII.

Fig. 12 shows the results of an ordination of the relative occurrences over the habitats by DECORANA, where the habitat groups mentioned above are indicated with dashed lines. The TWINSPLAN divisions form rather coherent groups. The first axis of DECORANA is clearly correlated with moisture, dry habitats: 15-16, coniferous forest; 6, Corynephorretum; 4, Calluna-heath on the left, and wet: 31-33, shore habitats on the right. The second axis seems to be related in some way with the structure of the vegetation, open vegetations: 1-5, heath and peat habitats, 6-11, dune habitats in the lower part, and highly shaded vegetations: 16-22, forests in the upper part of the figure.

Classification of species

The habitat preferences of the species are indicated by their relative occurrences over the 33 habitats. The species are divided into eight species groups: A-H (fig. 13), and are tabulated in tables 2-9. Most groups contained very eurytopic as well as rare species. These species have been taken from the original groups and are brought together into two separate tables: 8 (eurytopic species) and 9 (rare species).

Species group A (table 2): Species of heath vegetations and peat moor, mainly occurring in habitat group I.

Species group B (table 3): Species of sandy localities, such as dunes, arable land and coniferous plantations; principal occurrences in habitat-group II and/or III.

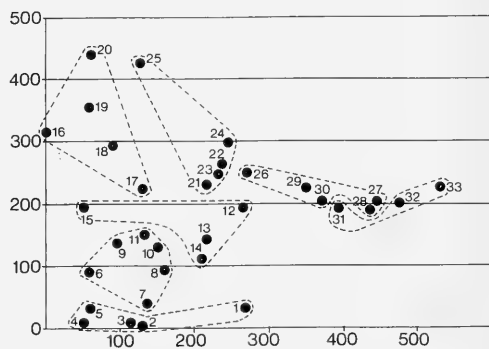


Fig. 12. Ordination by DECORANA, presenting on the first two axes the projections of the species scores for the 33 habitats (explanation see table 1). The dashed lines indicate the main habitat-groups: 1-5 = peat and heathland vegetations, 6-11 = poor grasslands and dune habitats, 12-15 = cultivated land and open coniferous plantations, 16-20 = mature forests, 21-25 = moist to wet forests and ruderal grassland habitats, including limestone grassland, 26-30 = moist habitats, reedland, pioneer (colonization-) habitats, polders, 31-33 = wet habitats, shores and river banks.

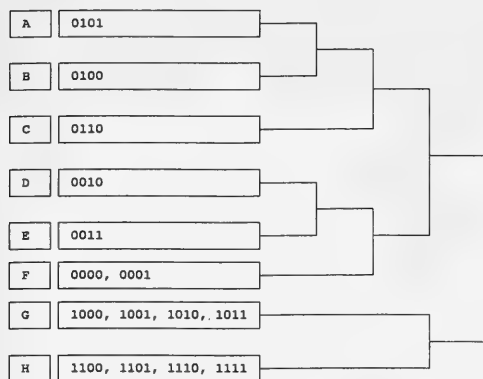


Fig. 13. Dendrogram of the species groups according to the TWINSpan classification. The letters A-H indicate the TWINSpan end-groups, treated in the respective species group. The numbers 0000-1111 indicate the first four levels of the TWINSpan classification (compare table 2-7).

Species group C (table 4): Species of open areas, dune localities as well as colonization sites and shores, mainly in habitat-groups II, III and/or VI, VII.

Species group D (table 5): Species of forests and/or ruderal places, including limestone grassland; occurrences mainly in IV and/or V.

Species group E, F, G (table 6): These groups are not treated separately, because the separate end-groups are rather heterogeneous and less typical for a certain habitat group than the other species-groups. However, many species occur in moist and shaded localities, such as moist forests, scrubs and reedland; having an accent in habitat groups V and VI, and others show no special preference for moist habitats.

Species group H (table 7): Species of more open moist-wet habitats, reedland and shores; occurrences mainly in groups VI and/or VII, (TWINSpan species end-groups 1100, 1101, 1110 and 1111).

Eurytopic species (EU) (table 8): These species are placed in a separate group on basis of their ecological amplitude: $PRES > 0.75$ or $SIM > 0.85$. The species are arranged according to their eurytopy estimates (Pres, Sim). The end-group number indicates from which of the species groups mentioned above (A-H) they originate.

Rare species (R) (table 9): Species have been placed in this group when the number of samples (Sa) < 6 and when the number of individuals < 50 . If the species is merely present in 3-5 year-samples and these samples belong to the same habitat, the species was not placed into group H.

In tables 2-9 relative occurrences are presented

according to the percentual scaling, where for each species the highest mean $\ln(SDY+1)$ in one of the 33 habitats, is put at 100%. In the body of the tables the numbers indicate: 1 = 5-15%; 2 = 15-25% etc., 9 = 85-95% and * = $> 95\%$ respectively. Points indicate the habitats where the species is present, but where the relative occurrences are below 5%.

Species were ordinated by DECORANA, according to their relative occurrences per habitat. In figs. 14-20 the position of the species belonging to the groups A-H on the first two axes of the ordination is given. The first axis shows a dry-wet gradient: species preferring dry habitats (group A) on the left (fig. 14), and species from wet habitats (group H) on the right (fig. 19). The second axis is related with amount of shade: species of exposed habitats (group A) at the bottom (figs. 14, 15), and forest dwelling species (group D) at the top of the figure (fig. 17). The highly eurytopic species of group EU, take a central position according to that of the other species groups, resembling that of the intermediary groups E, F and G (fig. 18).

Ecological amplitude, soil type and humidity

The indices for the ecological amplitude of the species (Pres, Sim), for soil preference (So) and humidity preference (Hu) are given in the right columns of the tables 2-9. Also the number of year-samples (Sa), the number of individuals (N).

DISCUSSION OF THE SPECIES GROUPS

In this chapter we will give a short discussion per species group. Analyses more into detail can be expected in further papers where the species composition of several habitats or habitat-groups will be treated.

Species-group A (table 2 p. 294)

Most species listed in table 2 show clear preferences for peaty soils and/or sandy soils. When they have no preference for any soil type, they are mainly restricted to oligotrophic habitats. The humidity preference varies: most species that also occur in the *Corynephorum*, such as *Pterostichus lepidus*, *Bradycellus ruficollis* and *Amara infima*, do not occur in humid habitats. Other species have a rather high preference for humid sites (humidity 4-5), such as *Pterostichus aterrimus*, *Agonum ericeti*, and *Anisodactylus nemorivagus*, which are known from literature as true peat-moor dwellers (Lindroth 1945, Mossakowski 1970a, 1970b). The results agree with those of investigations in German heath-moor complexes (Horion & Hoch 1954, Grosseappenberg et al. 1978). According to the TWINSpan-classification (figs. 4-5), peat moor has

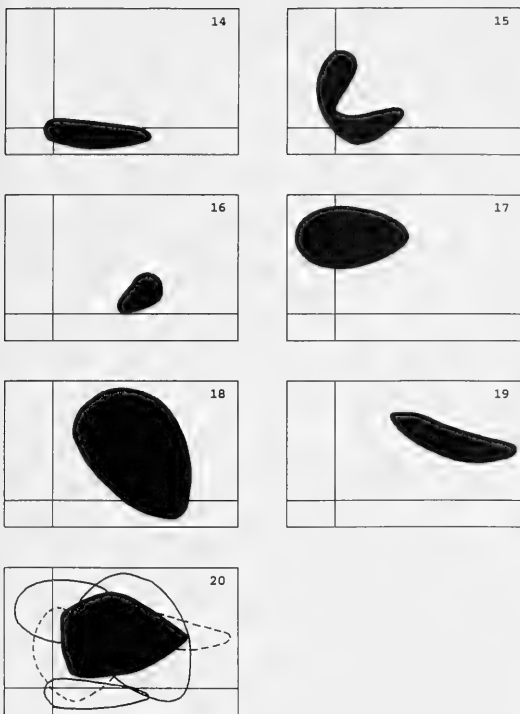


Fig. 14-20. Ordination of the species groups A-H and group EU, by DECORANA. – 14, group A: species of heath vegetations and peat moor (see table 2); 15, group B: species of sandy localities, dunes, arable land and coniferous plantations (see table 3); 16, group C: species of open areas (see table 4); 17, group D: forest species and species of ruderal places including limestone grasslands (see table 5); 18, groups E, F and G: species occurring in most and shaded habitats (see table 6); 19, group H: species of moist-wet habitats, reedland and shores (see table 7); 20, group EU: eurytopic species (see table 8); the outlines of the previous groups are indicated to accentuate the central position of the eurytopic species.

been included in the present species group and not in one of the moist groups E or F, in spite of the occurrence of many moist-preferring species. This can be explained by the fact that the fauna of peat-moor is rather poor in species and that the majority of these species is ecologically more related to heath-like vegetations. The peat-moor fauna has hardly any species in common with the carabid assemblages of shore habitats (species-group F), where the occurrence of many *Bembidion*-species is most characteristic. The results in table 2 agree well with those from the literature. Some studies carried out in Germany by Mossakowski (1970a, 1970b) and Rabeler (1947) also recognize *Agonum ericeti*, *Anisodactylus nemorivagus*, *Bradycellus ru-*

ficollis and *Trichocellus cognatus* as characteristic species for peaty soil. Mossakowski (1964, 1970c) and Rabeler (1947) mention some species characteristic for heath vegetations, such as: *Amara infima*, *B. ruficollis*, *Carabus arvensis*, *C. nitens*, *Cicindela campestris*, *Olisthopus rotundatus* and *Pterostichus lepidus*. Some of the species mentioned by these authors can be found in the ecologically most related species group B (table 3) or they are arranged among the eurytopic or rare species (tables 8-9), e.g. *Bembidion nigricorne*, *Bradycellus caucasicus*, *Cicindela sylvatica*, *Pterostichus versicolor*, *Syntomus foveatus* as well as several *Calathus* and *Cymindis* species.

Species group B (table 3, p. 294)

This group is divided into two subgroups, based on a sixth level TWINSPLAN division: B1 – species mainly occurring in the Corynephorum, dune habitats and poor grassland; B2 – species of sandy arable land, waste land and young coniferous plantations on sand. The species of group B1 are in general confined to poor, dry and open, sandy habitats especially in dune areas. Some species are very stenotopic and more or less restricted to drifting sands of coastal and inland dunes: *Harpalus servus*, *Harpalus vernalis*, *Masoreus wetterhali*, *Ophonus cordatus* and *Harpalus neglectus*. Some papers concerning dunes and Corynephorum sites (Schj t  Christensen 1957, 1966a, 1966b) mention several *Harpalus* species e.g.: *H. anxius*, *H. solitarius*, *H. neglectus* and *H. smaragdinus* as being typical for dry and sandy areas in Denmark. The following species can also be found in heath vegetations and they are obviously ecologically related to the species of group A: *Bembidion nigricorne*, *Cymindis macularis*, *Notiophilus germinyi* and *Cicindela sylvatica*. Most species in the B1 group have low humidity indices (1-2), and are rather stenotopic.

The species belonging to group B2 are characteristic for many types of sandy habitats. As far as they occur in cultivated areas, most of them avoid heavy fertilization. Species common to intensively cultivated agricultural land, can be found among the eurytopic species (see table 8). *Laemostenes terricola*, *Calathus micropterus* and *Pterostichus quadri-foveolatus* are also related to forests (habitat group IV).

Species group C (table 4, p. 295)

This small group consists of four species that occur primarily in open localities, dry as well as rather wet ones. *Clivina collaris* is predominantly a riparian species. The other species are confined to open country with a sparse vegetation and show a preference for coastal areas; this especially applies to *Calathus mollis*.

Species group D (table 5, p. 296)

Three subgroups were grouped together based on their occurrences in the main habitat groups IV and V: D1 – Stenotopic species of cultivated and ruderal sites such as poor unfertilized fields, gardens and limestone grasslands, mainly on limestone soil in the southern part of the province of Limburg; D2 – Species of more or less moist and shaded places partly on limestone soil; D3 – Eurytopic and stenotopic forest species.

Belonging to the first subgroup are several heath-preferring species (xerotherm species: Becker 1975, Lindroth 1949) which in The Netherlands are exclusively confined to limestone soil: *Parophonus maculicornis*, *Amara nitida*, *Brachinus crepitans*, *Harpalus dimidiatus*, and *Ophonus melleti*. Other thermophilous species can also be found on localities outside the limestone area of The Netherlands, on open sun-exposed, xerotherm sites such as slopes of river dikes with a southern exposition (Turin 1983, Turin et al. 1977): *Amara montivaga*, *Ophonus puncticeps*, *Harpalus rubripes*, and *Lebia chlorocephala*. *Ophonus rufibarbis* is the least thermophilous and most eurytopic *Ophonus* species. It can be found on more or less shady sites (Lindroth 1974, 1986).

The species of the D2 subgroup are restricted to the southern part of the province of Limburg or have a more or less fluviatile distribution in The Netherlands. Most species prefer chalky, clayish soil or loam, some of them inhabiting shaded (wooded) sites: *Stomis pumicatus*, *Bradycellus sharpi*, *Carabus coriaceus*, and *Pterostichus madidus*. These species also occur in limestone grassland at slopes with a northern exposition (Turin 1983).

Subgroup D3 consists of the true forest species. The first six species are rather eurytopic, which also applies to *Leistus rufomarginatus* and *Carabus problematicus*. Some of the more stenotopic forest species are more or less restricted to the oak-hornbeam forests of the southern part of Limburg and the easternmost part of The Netherlands, e.g. *Abax parallelus*, *Molops piceus*, and *Trichotichnus nitens*. *Amara praetermissa* can be found in the Corynephorum, but also at acid sites on top of the limestone hills in Limburg with a more heather-like (*Calluna*) vegetation, which explains the presence of this species in the D-group.

There are far more investigations into the composition of the carabid fauna of forests than in that of heathland vegetations. Nowadays heathland is rapidly disappearing from The Netherlands, but about a hundred years ago it was one of the most prominent components of the landscape. In 1850 the area covered with forest was below 3%. Afforestation, which started in the first part of this

century, has increased this area to about 6% in 1950 and 8-9% at the moment. Thus, many Dutch forests are rather young. The majority of this forested area consists of coniferous and exotic trees. Apart from the light oak-birch forests, which form the more natural climax vegetation on sandy soils, and the riverine forests, the more rich types of deciduous forest, e.g. *Quercus-Carpinetum*, can only be found in restricted areas. Species characteristic (Thiele 1977) of these kind of forests in Central Europe, e.g. *Abax ovalis* (not in pitfalls), *Carabus auronitens*, *Molops piceus*, *Pterostichus cristatus* and *Trichotichnus nitens*, are restricted to the very eastern and southern parts of The Netherlands. Thiele (1977) reviews studies on the most abundant species of the (sub)centreuropic forests, including many investigations from Germany, such as those of Heckendorf et al. (1986), Kolbe (1968, 1970), Lauterbach (1964), Rabeler (1957, 1962, 1963, 1967 and 1969) and Thiele (1956). Also literature concerning The Netherlands was taken into account by Thiele, e.g. Van der Drift (1959) and Den Boer (1965). Recently, Turin & Heijerman (1988) carried out a first survey on the present data in a more simple way by only examining the species having the highest numbers of individuals and presences in all types of forest in The Netherlands together, and arranging them according to the fraction of specimens caught in forests, as compared with those in other habitats. The terms 'stenotopic / eurytopic forest species' they use, only apply to the Dutch area. Especially the species of mountainous localities are missing (highest altitude in The Netherlands is below 400 m). Most stenotopic forest species mentioned by Turin & Heijerman are now listed in table 5. Heijerman & Turin (1989) found great differences in fauna composition between forests in different parts of The Netherlands. This can possibly be explained by the fact that most of the forested areas are rather young and have been colonized recently.

Species group E, F, G (table 6, p. 297)

This group is polythetic and in fact a compilation of seven small TWINSPLAN end-groups. The species predominantly occur in moist and shaded habitats. Most species are hygrophilous, reaching high numbers in wet grassy forests, moist grasslands and reedland: E1 – species of moist forests, sometimes in dune valleys and in moist grassland; F1 – two species of rather open and dynamic habitats; F2 – species of moist and shaded sites; G1 – only a single species; G2 – species with high numbers in reedland and in moist grassland, *Oodes belopoides* lives at wet and shaded sites; G3 – only *Bembidion obtusum*, which more or less prefers cultivated country; G4 – mainly hygrophilous spe-

cies of wet meadows, marshes and reedland. Most species in group G4 inhabit rather wet and dense, shaded vegetations. Exceptions are: *Amara ovata* and *A. famelica*, which both live in more open sites. Investigations into the fauna of moist and wet habitats are for reedland, swamps and lake shores: David & Marchal (1963), Dawson (1965), Jarmer (1971), Koch (1977), Obrel (1972), Renkonen (1944) and Wasner (1977). The present results largely agree with the studies mentioned.

Species group H (table 7, p. 298)

The species belonging to group H reach high numbers in the moist or wet habitat groups VI and VII. Subdivisions based on the TWINSpan classification are: H1 – a single rather eurytopic, colonizing species: *Amara similata*; H2 – mostly hygrophilous species of young habitats in polders and in other colonization sites; H3 – four species of open sites near water; H4 – Species of shore habitats, a number of them confined to saline localities. *Pterostichus cupreus* is similar to *Amara similata* in living in moist grassland and arable land, both species being rather eurytopic. *Bembidion bruxellense*, *Chlaenius nigricornis*, *Agonum albipes*, *Elaphrus cupreus* and *E. riparius* are characteristic of river meadows and reedland. *Amara convexiuscula* is a typical species of sea clay soil and found mostly along the coast, but it occurs, just as *Acupalpus exiguus*, *Lasiotrechus discus* and *Amara majuscula*, also in high numbers in the Dutch IJsselmeer polders (Turin et al. 1977). For large areas such as the Dutch polders, only constantly macropterous species and full-winged specimens of wing-dimorphic species are capable of colonizing such areas (Haack 1971, Meijer 1973, 1974, 1980). In colonization of small sites, such as burnings and clearings, also big wingless species may be able to immigrate (Szyszko 1986), but in general, pioneer communities can be characterized by their high numbers of winged species. An example of long-term colonization and succession of carabids along rather homogenous road verges on clay soil in three Dutch polders of different age is given by Haack et al. (1980). It illustrates that the carabid fauna of the Dutch polders keeps a coastal character for many decades.

Most species of the H4-group live close to water in open habitats. Several species of this group are restricted to the salt marshes of the Waddensea area and the islands of the province of Zeeland: *Dicheirotrechus gustavi*, *D. obsoletus*, *Pogonius chalcus*, *Bembidion normannum*, *B. pallidipenne*, *Dyschirius salinus*, *D. obscurus*, and *Bradycellus distinctus*. About saline habitats several studies are available: Heydemann (1962, 1967), Mossakowski (1971), Niemela (1988) and Rueda & Montes

(1987) and they mention several species as typical for this habitat. The species occurring in saline habitats in The Netherlands are all treated in Turin (1991).

Many of the characteristic and abundant species of inland shores and river banks cannot be found in Group H, since pitfalls do not function well in shore habitats. Especially focused on the riparian fauna of running water are the studies of: Andersen (1970, 1982, 1983), Krogerus (1948), Lehmann (1965) and Plachter (1986). Species living so close to the water that they hardly can be trapped with pitfalls are for instance: *Agonum micans*, *Bembidion doris*, *B. obliquum*, *Dyschirius aeneus* and *Nebria livida*. The species *Bembidion articulatum*, *B. punctulatum*, *B. semipunctatum* and *B. testaceum*, all from river banks and often abundant in The Netherlands, are not present in the pitfall material. Some shore species that also can be found at some distance of the water, are listed among the rare species (table 9).

Eurytopic species (table 8, p. 299)

A group of 53 eurytopic species and ubiquitous, extracted from all habitat groups on basis of their ecological amplitude. Most species in this group show high occurrences and abundances in one of the habitat groups III, V and/or VI. Apart from a few species, they do not clearly prefer a special soil type or humidity class. Some of them have high tolerances with respect to fertilizers and intensive agricultural management and can therefore be numerous in arable land and in pastures. Thiele (1977), who compared the carabid faunas of arable land, meadows / pastures and clover / alfalfa, in fact gives incomplete information of the species preferences. The species listed in Thiele's compilation are not characteristic for cultivated areas, but most of them simply are highly eurytopic species (see table 8). A similar survey was published by Basedow et al. (1976) and the results resemble those of Thiele.

Notiophilus biguttatus and *Nebria brevicollis* are eurytopic forest species that also occur in dense, shady grasslands and in other shaded sites, such as gardens and orchards (Turin & Heijerman 1988).

Rare species (table 9, p. 300-301)

A group of 59 rare species. Just as in the previous groups, the original TWINSpan end-groups (GR) are mentioned after the species names. Twenty-six of the species only occur in one kind of habitat. For some species a lack of data is the main cause that the information on the species preferences is incomplete. However, for many species that have a highly restricted distribution in The Netherlands, especially those living near the fringes of their

ranges, the relative occurrences shown in table 9 will give a reliable picture of the species preferences in the Dutch territory. The species of this group will be treated in a separate study.

DISCUSSION

Only a few studies concerning classification of carabid species based on a large dataset are known from western and north-western Europe. The most important are chronologically: Lindroth (1945, 1949), Thiele (1977), Den Boer (1977), Luff et al. (1989) and Eyre & Luff (1990a, 1990b).

Lindroth (1945, 1949) indicated species preferences for humidity, and certain vegetation types, such as woodland. Although his conclusions were based mainly on material from Fennoscandia, his classification proved to be valuable for a much larger area. It was used in many carabidological studies all over northern and western Europe. When comparing the results of the present study with Lindroth's classification (table 10), one can conclude that they correlate rather well. The xerophilous species (X) in groups A1, B1, B2, C1 and D1 (table 10), the hygrophilous species (H) in groups A1, G4, H2, H3 and H4 (table 10) and the forest species (HW+W+WA) of Lindroth are found in groups D2, D3 and E1. Lindroth's mesophilous and more or less ubiquitous species (N) are scattered over a wide range of our species-groups with the highest numbers in the eurytopic EU-group (table 10). Fifty-nine species mentioned by Lindroth were caught in pitfalls in too low numbers for a characterization (group R) and 85 of the Dutch species mentioned by Lindroth, were not caught in pitfalls at all in The Netherlands (table 10 group O). From Lindroth's characterizations (table 10) we can conclude that these species that could not be characterized in the present study, belong to the inhabitants of shores and river banks (80 species, table 10). Others are very rare or even extinct in The Netherlands, e.g. many xerophilous species (see Desender & Turin 1989, Turin 1990).

Thiele (1977) attempted to characterize the carabid faunas of certain habitat groups such as forests, cultivated land and sandy habitats, comparing them on basis of species presence. He mainly used literature sources from the entire northwestern part of Europe. Although he included several lowland and mountain forests for the characterization of the forest fauna, we feel that this method gives an incorrect picture of the species preferences, especially because the relative occurrences and abundances in other localities were not taken into account.

Den Boer (1977) gives a far more complete picture for 75 of the most abundant species in his

study area, by listing the data of hundreds of year-catches in many kinds of habitat in the province of Drenthe (The Netherlands). However, his study area is rather limited and many Dutch habitats and soil types are absent from his study (e.g. coastal dunes, clay soil and limestone grasslands). A comparison with Den Boer's results is not appropriate here, because his data form a significant part of our data set.

Several extensive studies on classification of carabid species have been published recently. Luff et al. (1989) is related to the classification of carabid habitats in north-east England, while another deals with the ground beetles of grassland habitats in Europe (Eyre & Luff 1990a). Finally, Eyre & Luff (1990b) presented a classification of ground beetles of the British grasslands in more detail. In all studies DECORANA and TWINSpan were used as statistical methods. For the first study (Luff et al. 1989), very heterogeneous material from 248 sites in North-East England was used, primarily collected for use in the British mapping scheme. Ten habitat groups were recognized based on the distribution of the species presence over the sites. A method was developed to fit in new sites. A first limitation of this method is that new sites can only be fit in using species that already contributed to the original ordination. Secondly, that only presence/absence data can be used. The original data set consists both of data from pitfalls, and sampling by hand. The possibility to include also samples from localities where pitfalls do not function, such as shore habitats, certainly is an advantage when using only the species presence. A main disadvantage is that the species' relative occurrences cannot be taken into account. The study of Luff et al. is, as they also notice in their discussion, in the first place a methodological one and the results do not give a definitive and complete picture of carabid habitats of the British Isles. Many habitats, for instance woodland, will have to be investigated more intensively. Three of the ten habitats do not occur in The Netherlands (upland dry, upland wet and boulder). The remaining habitat groups are rather broadly defined: coastal, woodland, dry grassland, wet grassland, wet running, wet still – silt, wet still – sand. It is rather difficult to compare the species preferences for British habitats with the present results, although many species preferences seem to correlate well, e.g. those of *Calathus erratus*, *Amara bifrons*, *Calathus rotundicollis* and those of many eurytopic species such as *Calathus melanocephalus*, *Loricera pilicornis*, *Pterostichus nigrata* and *Trechus obtusus*. From the present classification it can be learned that the most important environmental factor influencing the ordination of carabid species is soil moisture (fig. 14). This is in support of the

analyses by Luff et al. (1989). It is therefore very plausible that carabids are good indicators for moisture conditions in the field.

In the study concerning the heathland and grassland habitats in northern and central Europe, Eyre & Luff (1990a) used material from 638 heath and grassland pitfall sites. A number of these sites have also been used in the present study. Classification with TWINSpan resulted in the identification of 17 habitat groups. In this study, woodland sites as well as shore habitats were not included. Although it is not easy to compare this classification with the present results, it is clear that some primary divisions are similar, e.g. heath, cultivated land and polders (pioneer habitat sites).

The classification of Eyre and Luff (1990b) concerns the classification of British grasslands. The data consist of material from all over England, Wales and Scotland. The results are to some extent supporting the present analysis. 'Dry' species, such as *Broscus cephalotes*, *Calathus mollis* and *C. fuscipes* are found in the same habitats in Britain. Also heath and peat-moor species (group A, table 2) have been placed in similar habitat groups in the analysis of Eyre & Luff. Some species that are recognized as woodland species in the present analysis, are scattered over many habitat groups in the British study. This is probably because mature woodlands have not been taken into account. In the results of both British studies (Eyre & Luff 1990b, Luff et al. 1989) some species preferences differ obviously from the situation in The Netherlands, e.g. the above mentioned species *Carabus violaceus*, *Pterostichus cristatus* and *P. madidus* seem to be much more eurytopic in England.

In their discussion Eyre and Luff (1990a) mention the scale problem, stating that the greater the area covered by a study, the less precise the results will be. It is obvious that in such a case the classification will be influenced by the geographical distribution of the species. A geographical component is even present within a relatively small study area as The Netherlands, where, for instance, *Pterostichus madidus* occurs only in the southern and central part of The Netherlands. The mean $\ln(\text{SDY}+1)$ in our method, however, is calculated over all samples of a certain habitat, also those situated outside the range of *P. madidus*. This problem applies to all species with a restricted distribution within a certain study area. The problem becomes more pressing, however, when the study area is still larger, because the relative number of species with restricted distributions will increase. On the other hand too small areas such as the province of Drenthe in The Netherlands (Den Boer 1977) contain not enough habitats to make a classification useful.

The present results will probably surprise experienced carabidologists to some extent. Several species show rather unexpected occurrences. *Abax parallelepipedus*, for instance, is a species characterized by many authors as restricted to forests, forest edges and hedges (Koch 1989, Lindroth 1986, Thiele 1977, Turin & Heijerman 1988), but appears to occur in a wide range of habitats abundantly, and in an even wider range in low numbers. It is a well known fact that species preferences for certain types of vegetation (habitats) can shift over geographical distance or at different altitudes. *Pterostichus cristatus*, for instance, is an inhabitant of cool mountain Fagetalia forest (Thiele 1977), but it also occurs in open, moist sites in Cumberland and Northumberland in the British Isles (Lindroth 1974). *Pterostichus madidus*, which inhabits the Fagetalia and Quercus-Carpinetum (oak-hornbeam forest) (Koch 1989, Thiele 1977) in Central Europe, prefers open country and cultivated soil in the British Isles (Lindroth 1974, Eyre & Luff 1990a, Luff et al. 1989). In The Netherlands it takes an intermediate position (table 5). In the southern part of the province of Limburg *P. madidus* is the most abundant species in the forest edges of the oak-hornbeam forest, but it also occurs quite frequently and abundantly in shaded meadows and limestone grasslands without an extremely southern exposition. In the central part of The Netherlands it can only be found in light forest and in low numbers. The above mentioned differences between the present classification and that of British Isles will partly be due to such geographical differences in species habitat preferences.

We support the conclusion of Eyre & Luff (1990a) that classifications based on large datasets, together with the data from pitfall sampling from all over Europe, make carabid beetles a reliable group for environmental monitoring.

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TABLES

Table 1. The 33 habitats recognized by the 'ecocode', and per habitat, the numbers of year-samples and the number of sites where pitfall series were situated.

NR	HABITAT	SAMPLES	SITES
		n	n
1	Peat moor (wet, Sphagnum)	16	9
2	Heath with <i>Molinia</i> (moist)	28	9
3	<i>Erica</i> heath (moist)	14	7
4	<i>Calluna</i> heath (dry)	101	27
5	Heath with grasses, <i>Deschampsia</i> (dry)	119	26
6	<i>Corynethoretum</i> (dry, open)	65	24
7	Coastal dunes (dry, open)	53	20
8	Dune grassland (coastal)	69	29
9	Dune forest (coastal)	68	13
10	Dune scrub (coastal)	100	51
11	Poor grassland on sandy soil (inland)	23	14
12	Cultivated, pasture (inland, sand, fertilized)	33	22
13	Cultivated, arable (inland, sand, fertilized)	17	17
14	Cultivated, waste land (inland, sand)	26	11
15	Coniferous forest, plantation (open)	15	12
16	Coniferous forest, mature	65	64
17	Coniferous forest, old (moist)	11	11
18	Deciduous forest, oak-birch	126	73
19	Deciduous forest, oak-beech	41	34
20	Deciduous forest, oak-hornbeam	17	17
21	Deciduous forest, poplar (moist, polders)	19	13
22	Deciduous forest, alder-willow (moist-wet)	42	40
23	Inland scrub (moist)	44	22
24	Ruderal, park, orchard (dynamic)	40	40
25	Limestone grassland, dike slopes (xerotherm)	54	54
26	Grassland with herbs (inland, unfertilized)	98	70
27	Reedland, Lauwersmeer polder (sand-silt)	18	4
28	Reedland, IJsselmeer polder (sea clay)	52	22
29	Cultivated, IJsselmeer polder (sea clay)	52	26
30	Colonization sites, building lands (recent)	35	15
31	Sand banks near salt water, seashore (open)	93	40
32	Inland shores, river banks (open)	22	6
33	Salt marshes (sea clay)	40	20

Tables 2-9. The tables show the distribution of species relative occurrences over the 33 habitats recognized.

Explanation

A-H. – Tables 2-7, show the main species groups A-H, recognized by TWINSpan classification. The sub-division of the main species-groups B and D is based on a sixth level, and those of groups E, F, G and H is based on a fourth level TWINSpan division.

EU, RA. – The tables 8 and 9 show respectively the eurotopic (EU) and rare (RA) species, which have been separated from the main groups A-H. Eurytopic species ($\text{Pres} > 0.75$ or $\text{Sim} > 0.85$), have been placed into one group (table 8) to get a more clear picture of the most typical species of the principal groups A-H. The rare species have been separated from these groups for statistical reasons. They occur in too low numbers in The Netherlands ($\text{Sa} < 6$ and $\text{N} < 50$, except when all were found in the same habitat), to get a reliable picture of the species habitat preferences

NUM. – Species numbers. The full names with references to this number, can be found in the index

GR. – In tables 2-7 in this column the species group subdivision is indicated. In tables 8 and 9 the letters A-H refer to the original primary group where the eurytopic and rare species were placed by TWINSpan classification

I-VII. – In the heading of the tables: main habitat groups that have been recognized by TWINSpan classification (see fig. 4).

1-33. – In the heading of the tables: habitats, explanation see table 1.

1-9 and *. – In the body of the table, give relative occurrences according to the percentual rescaling per species (see text): '1' = $\ln(\text{SDY}+1) \leq 5\%$, '1' = $5\% < \ln(\text{SDY}+1) \leq 15\%$, '2' = $15\% < \ln(\text{SDY}+1) \leq 25\%$, '3' = $25\% < \ln(\text{SDY}+1) \leq 35\%$, etc., '9' = $85\% \leq \ln(\text{SDY}+1) < 95\%$, '*' = $95\% \leq \ln(\text{SDY}+1) \leq 100\%$ (This value stands for the $\ln(\text{SDY}+1)$ value that is put to 100%, which was the highest value of that species)

Pres. – Eurytopy estimation based on species presences: a low value means that the species is present in a low number of the 33 habitats; 1 means that the species is present in all habitats).

Sim. – Eurytopy measure based on the index of SIM D-1 (a low value means that the species is very stenotopic; highest value=0.94).

So. – Soil-preference measure, based on mean $\ln(\text{SDY}+1)$ figures; soil type / (all other soil types) > 2 , otherwise no indication of soil preference is given: c = riverclay + seaclay, li = limestone, ll = limestone + loam, lo = loam, ls = loamy sand / sandy clay, pm = peatmoor, rc = river clay, sa = sand, sc = sea clay, sm = sand + peatmoor.

Hu. – Humidity-preference measure (dry 456 samples, moist 690 samples, wet 461 samples), based on mean $\ln(\text{SDY}+1)$. 1 = mainly in dry samples [$\text{dry} > 10 \times (\text{moist} + \text{wet})$], 2 = not in wet samples [$\text{dry} + \text{moist} > 20 \times (\text{wet})$], 3 = not in dry and not in wet samples [$\text{moist} > 10 \times (\text{dry} + \text{wet})$], 4 = not in dry samples [$\text{wet} + \text{moist} > 20 \times (\text{dry})$], 5 = mainly in wet samples [$\text{wet} > 10 \times (\text{dry} + \text{moist})$]

Sa. – Number of year-samples

N. – Number of specimens.

	B1	1	2	5	6	*	7	.	1	.	2	.	.	.	1	.	.36	.82	sa	2	161	457
Panageus bipustulatus	B1	.	3	3	.	2	.	.	139	.68	sa	1	203	486
Harpalus servus	B1	.	1	3	*	1	.	1	.	1	136	.73	sa	1	98	540
Harpalus vernalis	B1	.	1	3	*	1	4	.	136	.65	sa	2	123	881
Harpalus xanthopus	B1	.	.	.	*	4	336	.78	sa	2	143	653
Masoreus wetterhali	B1	.	1	9	.	.	1	727	.50	pm	2	103	5612
Bembidion nigricorne	B1	.	5	*18	.38	sa	1	691	712
Cymindis macularis	B1	.	2	142	.74	sm	2	291	2507
Notohippus germinyi	B1	1	1	*	312	.51	sa	2	17	106
Cymindis humeralis	B1	7	.	127	.74	sa	2	105	559
Amara lucida	B1	.	1	2	9	.	5	.	*	.	312	.68	sa	1	8	26
Harpalus picipennis	B1	.	.	6	.	*	306	.03	sa	1	2	72
Amara erynota	B1	.	.	.	*	*09	.26	sa	1	13	49
Ophonus cordatus	B1	.	.	.	*	118	.26	sa	1	14	290
Harpalus neglectus	B1	1	*09	.25	.	.	14	24
Cicindela sylvatica	B1	1	14	24
Amara anthobia	B2	.	.	5	5	.	.	.	*24	.78	sa	2	21	256
Brosicus cephalotes	B2	.	2	1	*61	.53	2	160	3413	
Harpalus distinguendus	B2	1	*21	.25	sa	2	13	37
Laemostenus terricola	B2	1	*33	.67	2	43	381	
Leius spinibarbis	B2	.	3	1	*24	.49	2	34	676	
Nebria salina	B2	.	1	2	.	145	.63	sm	119	1355	
Amara consularis	B2	7	*24	.51	sa	3	40	201
Amara fusca	B2	*03	.00	3	9	29	
Harpalus anxius	B2	1	1	*	.	1	.	.	4	233	.70	sa	1	43	144
Harpalus smaragdinus	B2	7	*	133	.59	sa	2	33	201
Calathus cinctus	B2	130	.42	sm	2	52	1186
Harpalus froelichi	B2	*03	.00	sa	3	5	19
Harpalus rufipalpis	B2	.	1	1	.	.	4	.	1	*45	.65	lo	2	101	895
Calathus micropterus	B2	.	1	1	2	142	.59	sa	2	92	1553
Perost. quadريفoveolatus	B2	1	*	1	139	.38	sm	56	1553	

Species group C1		I			II			III			IV			V			VI			VII																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
GR	NUMUSpecies	1	2	3	4	5																															
61	Amara tibialis						1	4			1	2																									
62	Clivina collaris	3																																			
63	Amara quenseli						*						3	*	3																						
64	Amara fulva						1								*																						
65	Calathus mollis							5	2		5				1																						

Table 6. Miscellaneous species, mainly of moist-wet, shaded sites (E1,F2), reedland (G2), marshes and wet meadows (G4) and related species (F1,G1,G3).

[illegible]

Table 8. Eurytopic species.

Eurytopic species, ubiquitous, EU																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																			
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Table 8. (continued).

219	<i>Calathus melanocephalus</i>	A	.	2	.	7	6	3	1	2	.	2	2	2	*	2	3	.	1	1	.	.	1	.	.	4	.	.	1.00	.91	sm	874	78250	
220	<i>Notiophilus biguttatus</i>	D	2	1	.	.	1	.	5	7	*	8	585	.91	.	446	7507		
221	<i>Agonum muelleri</i>	G	.	1	.	.	1	.	1	9	.	3	1	1	1	.	2	6	1	1	5	5	.	.	5	6	*	1	.	.85	.91	.	225	725		
222	<i>Calathus fuscipes</i>	B	.	1	1	2	6	2	*	1	4	9	.	.	7	*	7	8	.	3	1	.	.	1	1	3	2	4	4	1	7	1	4	2	.	.88	.92	.	575	23387	
223	<i>Harpalus rufipes</i>	E	.	.	3	2	1	1	*	5	9	5	.	1	.	.	.	1	2	5	2	4	1	4	1	7	1	4	2	.	1.00	.93	.	532	5656
224	<i>Loricera pilicornis</i>	H	5	3	2	.	1	1	2	2	.	3	3	2	1	.	2	8	4	*	6	2	3	.	1.00	.93	.	685	7387
225	<i>Amara communis</i>	G	1	3	1	1	2	.	.	1	3	4	2	2	9	.	3	5	1	1	1	2	2	.	2	3	3	.	1	*	4	1	1	5	.	.97	.93	.	704	12776	
226	<i>Nebria brevicollis</i>	E	.	3	1	1	1	.	1	.	1	.	1	2	7	2	3	*	1	5	4	4	7	.	3	6	4	4	2	.	.	5	2	1	.	.97	.94	.	665	30853	

Table 9. Rare species

Rare species, RA		I					II					III					IV					V					VI					VII					Pres					Sim					So					Hu					Sa					N																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
GR		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																					

257 *Pterostichus gracilis*
258 *Dromius quadrisignatus*

Table 10. A comparison between the classification made by Lindroth (1945, 1949, 1985 and 1986) for Fennoscandia and the present classification. The figures indicate the number of species that belong to the respective ecological groups. The columns A1-H4, EU, and RA in the heading of the table, refer to the species groups in the present classification (see tables 2-9). O = species common to Scandinavia and the Netherlands, but not present in the Dutch pitfall material. The rows in the table present the figures for the ecological groups of Lindroth: X = xerophilous species, N = ruderal and ubiquitous species, H = hygrophilous species, W = forest species and A = arboreal species.

Group	A1	B1	B2	C1	D1	D2	D3	E1	F1	F2	G1	G2	G3	G4	H1	H2	H3	H4	EU	RA	O	Sum
X	12	17	12	3	9		2		1	1	1								12	15	19	104
NX			1		1	1													1			1
N	2	2		N	1			1				1		1	1	2	1		18	4	3	5
NH	1		1			2	1		1							2			8	1	1	37
HW	7	1		1	2	1	1	1	1			3		11		16	3	17	7	31	49	18
H						2	1	2		1									6	4	6	153
HW	2					3	1	1	1										6	4	6	24
W		1	1			3	11	1											1	4	6	28
W/A																						
Sum	24	21	15	4	13	9	16	5	2	4	1	3	1	12	1	20	4	17	53	59	85	

Alphabetic list of species names with index to tables 2-9

Abbreviations: NUM = species number (table 2-9); So = soil preference; Hu = humidity preference; GR = species group; T = table number. For explanation see table 2-9, pp. 293-301.

Species	NUM	So	Hu	GR	T	Species	NUM	So	Hu	GR	T
<i>Abax carinatus</i> (Duftschmid)	245			5 RA	9	<i>Amara infima</i> (Duftschmid)	22	sa	2	A1	2
<i>Abax parallelepipedus</i> (Piller & Mitterpacher).....	91	ll		D3	5	<i>Amara lucida</i> (Duftschmid)....	40	sa	2	B1	3
<i>Abax parallelus</i> (Duftschmid)	94	ll	3	D3	5	<i>Amara lunicollis</i> Schioedte.....	193			EU	8
<i>Acupalpus brunnipes</i> (Sturm)	275			RA	9	<i>Amara majuscula</i> Chaudoir.....	142	sc		H2	7
<i>Acupalpus consputus</i> (Duftschmid).....	273		5	RA	9	<i>Amara montivaga</i> Sturm.....	67	li	2	D1	5
<i>Acupalpus dubius</i> Schilsky.....	1	pm	5	A1	2	<i>Amara nitida</i> Sturm.....	74	lo	2	D1	5
<i>Acupalpus elegans</i> (Dejean)	281			RA		<i>Amara ovata</i> (F.).....	122			G4	6
<i>Acupalpus exiguus</i> (Dejean)....	136	sc	4	H2	7	<i>Amara plebeja</i> (Gyllenhal).....	211			EU	8
<i>Acupalpus flavicollis</i> (Sturm)	116	ls	5	G2	6	<i>Amara praetermissa</i> (C.R. Sahlberg).....	103	li	2	D3	5
<i>Acupalpus meridianus</i> (L.).....	105	li		E1	6	<i>Amara pseudocommunis</i> Bu-rakowski.....	98	pm	4	D3	5
<i>Acupalpus parvulus</i> (Sturm)	152	ls	5	H2	7	<i>Amara quenseli</i> (Schoenherr)	63			C1	4
<i>Agonum albipes</i> (F.).....	140	ls	4	H2	7	<i>Amara similata</i> (Gyllenhal)....	132	c		H1	7
<i>Agonum assimile</i> (Paykull)....	182			EU	8	<i>Amara spreta</i> Dejean.....	179			EU	8
<i>Agonum dorsale</i> (Pontoppidan).....	174			EU	8	<i>Amara strenua</i> Zimmermann	261		1	RA	9
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<i>Agonum krynickii</i> (Sperk)....	11	pm	4	A1	2	<i>Asaphidion flavipes</i> (L.).....	177			EU	8
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<i>Harpalus rubripes</i> (Duftschmid).....	70	li		2 D1	5	<i>Panagaeus bipustulatus</i> (F.)....	31	sa	2	B1	3
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The 'Tijdschrift voor Entomologie' (Netherlands Journal of Entomology) has a long tradition in the publication of original papers on insect taxonomy and systematics. The editors particularly invite papers on the insect fauna of the Palaearctic and Indo-Australian regions, especially those including evolutionary aspects e.g. phylogeny and biogeography, or ethology and ecology as far as meaningful for insect taxonomy. Authors wishing to submit papers on disciplines related to taxonomy, e.g. descriptive aspects of morphology, ethology, ecology and applied entomology, are requested to contact the editorial board before submitting. Usually, such papers will only be published when space allows.

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- 74 Emmet, A. M., 1991. The scientific names of the British Lepidoptera. Their history and meaning. [E. J. van Nieukerken]. • Rubtsov, I. A., 1990. Blackflies (Simuliidae). – Fauna of the USSR. Diptera, Vol. 6, Part 6. [J. van Tol].

- 154 Kime, R. D., 1990. A provisional atlas of European Myriapods. Part 1. – Fauna Europaea Invertebrata, Volume 1. [P. J. van Helsdingen]. • Cherepanov, A. I., 1990. Cerambycidae of Northern Asia. Volume 1-3. [J. van Tol]. • Veeresh, G. K., B. Mallik & C. A. Viraktamath (eds.), 1990. Social insects and the environment. Proceedings of the 11th International Congress of IUSSI 1990.
- 200 Knight, W. J. & J. D. Holloway (Eds), 1990. Insects and the rain forests of South East Asia (Wallacea). [J. van Tol].
- 268 Moller Pillot, H. K. M. & R. F. M. Buskens, 1990. De larven der Nederlandse Chironomidae (Diptera). Deel C: Autoekologie en verspreiding. [A. W. M. Mol].

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INSTRUCTIONS TO AUTHORS

The *Tijdschrift voor Entomologie* publishes original papers dealing with systematic and evolutionary entomology. The editors particularly invite papers on the insect fauna of the Palaearctic and Indo-Australian regions, especially those including evolutionary aspects e.g. phylogeny and biogeography, or ethology and ecology as far as meaningful for insect taxonomy. Authors wishing to submit papers on disciplines related to taxonomy, e.g. descriptive aspects of morphology, ethology, ecology and applied entomology, are requested to contact the editorial board before submitting. Usually such papers will only be accepted when space allows.

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Johansson, R. & E. S. Nielsen, 1990. Tribus Nepticulini. — In: Johansson, R. et al. The Nepticulidae and Opostegidae (Lepidoptera) of NW Europe. — *Fauna entomologica scandinavica* 23: 111-238, pls.

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- 200 Knight, W. J. & J. D. Holloway (Eds), 1990. Insects and the rain forests of South East Asia (Wallacea). [J. van Tol].
- 268 Moller Pillot, H. K. M. & R. F. M. Buskens, 1990. De larven der Nederlandse Chironomidae (Diptera). Deel C: Autoekologie en verspreiding. [A. W. M. Mol].



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